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Taxonomy and phylogeny of the *Auriculariales* (Agaricomycetes, Basidiomycota) with stereoid basidiocarps

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Abstract

In the present study, we investigate taxonomy of the *Auriculariales* with effused or cupulate, persistent basidiocarps; generic and species concepts are revised based on morphological and DNA evidences. The genus *Eichleriella* is reinstated to embrace ten closely related species with ellipsoid-ovoid basidia, and the genus type, *E. incarnata*, is placed to the synonyms of *E. leucophaea*. *Eichleriella bactriana*, *E. desertorum* and *E. sicca* are described as new to science. In addition, four species earlier treated as members of *Exidiopsis* or *Heterochaete* are combined to the genus. The genus name *Heteroradulum* (type *Radulum kmetii*) is introduced for seven species with large, obconical, stipitate basidia. Of them, *H. adnatum* and *H. semis* are described as new. Two new genera, *Amphistereum* (with two species, type *Eichleriella schrenkii*) and *Sclerotrema* (monotypic, type *Exidiopsis griseobrunnea*), are proposed; *Hirneolina* (monotypic, type *H. hirneoloides*) and *Tremellochaete* (with two species, type *Exidia japonica*) are restored as good genera. The type species of *Heterochaete*, *H. andina*, is congeneric with *Exidiopsis* (type *E. effusa*).

Key words. Heterobasidiomycetes; internal transcribed spacer; perennial basidiocarps; wood-inhabiting fungi

1. Introduction

The *Auriculariales* are an order of the *Agaricomycetes* (Basidiomycota) which has been introduced as a result of morphological, cytological and phylogenetic studies (Bandoni 1984, Weiss & Oberwinkler 2001, Hibbett et al. 2014). Alongside the so-called jelly fungi (*Auricularia*, *Exidia* etc.), it embraces a number of corticioid, hydnoid and poroid genera. Traditional generic division within the order rested on macroscopic (the fructification type) and microscopic (type of basidia, presence of sterile hymenial cells etc.) characters has not been revised so far although recent DNA-based studies questioned a monophyly of some accepted genera (Weiss & Oberwinkler 2001, Sotome et al. 2014).

The *Auriculariales* are wood-decomposers inhabiting various hosts, from the tropics to the subartic zone. Some of them are able to survive under extreme climatic conditions, in particular, in arid regions or dry habitats. Two main strategies to persist the drought occur in the order. The first one is represented by genera *Auricularia* and *Exidia*: their gelatinous basidiocarps are able to dry out and revive again during the raining season. This feature is not unique to the *Auriculariales* since fructifications of the same kind are known in the *Dacrymycetes* and *Tremellomycetes*. The second

strategy is to develop steady, in some cases perennial fruitbodies, resuming their growth under favourable conditions (the so-called stereoid basidiocarps in a case of non-poroid species). Species with stereoid basidiocarps are widely distributed in many orders of the *Agaricomycetes*, although they are certainly a minority in the *Auriculariales*. They have been conventionally addressed to genera *Eichleriella* and *Exidiopsis* (Burt 1915, Wells 1961, Raitviir & Wells 1966, Wells & Raitviir 1980). No attempts to introduce phylogenetically reliable concepts of these genera have been performed yet. Therefore, the aim of the present study is to re-evaluate species and genus concepts of the stereoid *Auriculariales*, and define their main phylogenetic lineages.

2. Material and methods

Fungal collections. Type specimens and collections from herbaria H, LE, S, O, CFMR, TAAM, K, FH, NY, PRM, CWU, TNS, PC, GB, TENN were studied. Herbarium acronyms are given according to Thiers (2016). Morphological routine of this study follows Miettinen et al. (2012). In all cases, 20 tramal hyphae, 20 basidia and 20–30 basidiospores per specimen were measured. For presenting measurements, 5% extreme values from both ends of variation are given in parentheses. The following abbreviations are used in descriptions below: L – mean spore length, W – mean spore width, Q – L/W ratio, n – number of measurements per specimens; CB (+) means a presence of moderate cyanophilous reaction in Cotton Blue. Specimens sequenced for this study are marked by asterisk (*).

DNA extraction, PCR and sequencing. In total, 51 dried specimens from Europe, Africa, Asia and North America were selected for molecular sampling (Table 1). DNA was extracted from small fragments of dried basidiocarps. The procedure of DNA extraction completely corresponded to the manufacturer's protocol of the NucleoSpin Plant II Kit (Macherey-Nagel GmbH & Co. KG).
The following primers were used for both amplification and sequencing: ITS1F-ITS4 (http://www.biology.duke.edu/fungi/mycolab/primers.htm) for ITS region; primers JS1 (Landvik 1996) and LR5 (http://www.biology.duke.edu/fungi/mycolab/primers.htm) for LSU region. PCR products were purified using the Fermentas Genomic DNA Purification Kit (Thermo Scientific, Thermo Fisher Scientific Inc., MA, USA).

Sequencing was performed with an ABI model 3130 Genetic Analyzer (Applied Biosystems, CA, USA) using the BigDye Terminator Cycle Sequencing Ready Reaction Kit. Raw data were processed using MEGA 6 (Tamura et al. 2013).

Sequence alignment and phylogenetic analyses. In addition to 96 newly produced sequences (48 nrITS and 48 nrLSU), 23 nrITS and 35 nrLSU (including outgroups) sequences were retrieved from GenBank (http://www.ncbi.nlm.nih.gov/Genbank/) (Table 1).
Both nrITS and nrLSU sequences were aligned using the MAFFT online version 7 (Katoh & Toh 2008), with the Q-INS-i strategy (http://mafft.cbrc.jp/alignment/server/). For nrITS + nrLSU phylogeny, ambiguously aligned regions in ITS dataset were identified and excluded from the alignment for the subsequent analyses using TrimAl software (Capella-Gutierrez et al. 2009). In a few cases, alignments were adjusted manually using MEGA 6. Two different datasets were assembled for the phylogenetic analyses – nrITS (for *Eichleriella* and *Heteroradulum* spp.) and nrITS + nrLSU (for major clades of the *Auriculariales*). Alignments are deposited in TreeBASE: S20135 (nrITS dataset) and S20134 (nrITS + nrLSU dataset).

Phylogenetic reconstructions have been performed for all datasets with Maximum Likelihood (ML), Bayesian Inference (BI) and Maximum Parsimony (MP) analyses. *Auricularia mesenterica*

(voucher FO 25132) and *Sistotrema brinkmannii* (isolate 236) were used as outgroups (Table 1). Before the analyses, the best-fit substitution models for the alignment were estimated for each dataset based on Akaike Information Criterion (AIC) using FindModel web server (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html). In both BI and ML analyses for nrITS and nrITS + nrLSU datasets the model employed was GTR+G. ML analysis was run in the PhyML server, v. 3.0 (http://www.atgc-montpellier.fr/phyml/), with one hundred rapid bootstrap replicates. BI analysis was performed using MrBayes 3.1 (Ronquist & Huelsenbeck 2003) software for two independent runs, each with 10 million generations with sampling every 100 generations, under described model and four chains. MP analysis was performed using PAUP*4.0.b10 (Swofford 2002). One hundred heuristic searches were conducted by stepwise addition with random sequence addition and tree bisection-reconnection (TBR) branchswapping algorithm. One tree was held at each step during stepwise addition and the number of trees retained was limited to 100. Parsimony bootstrap analysis was performed with 1000 replicates. Gaps were treated as missing characters. The evolutionary pairwise distance between ITS sequences was assessed using MEGA 6 with GTR model.

3. Results

3.1. Phylogenetic analysis

nrITS + nrLSU general phylogeny. The final general nrITS + nrLSU alignment contained 1004 characters (including gaps). The overall topologies of the ML and BI trees were almost congruent. Seven major, strongly supported clades corresponding to morphological genera are defined in this study (Fig. 1):

(A) *Heterochaete hirneoloides* clade contains the sole species, a deviating member of *Heterochaete* s.l. The genus name *Hirneolina* is resurrected for it.

(B) *Eichleriella leveilleana – E. schrenkii* clade (pp = 1, bs = 96%). These two species with sturdy, dimitic basidiocarps form their own lineage in the *Auriculariales*. Therefore, they are placed to the genus *Amphistereum* described below.

(C) *Eichleriella* s.str. clade (pp = 1, bs = 88%). This group encompasses the genus type of *Eichleriella*, *E. incarnata* (considered a synonym of *E. leucophaea* – see below), as well as *E. alliciens*, *Exidiopsis macrospora*, *Heterochaete shearii*, and *H. tenuicula*, as they are defined in the modern literature.

(D) *Tremellochaete* clade is represented by the genus type, *T. japonica*. According to our data, *Tremellochaete* is not closely related to *Exidia* nor to *Heterochaete* where it has been addressed to, and, therefore, kept in its own genus.

(E) *Eichleriella deglubens* clade (pp = 1, bs = 90%). Traditionally addressed to the genus *Eichleriella*, *E. deglubens* s.l. constitutes a separate clade together with other, *Heterochaete*-like fungi. The genus name *Heteroradulum* is applied to this clade.

(F) *Exidiopsis effusa – Heterochaete andina* clade (pp = 1, bs = 100%). This lineage covers two species, *E. effusa* and *H. andina*. For the present study, we were able to obtain a newly generated nrLSU sequence from the type specimen of *Heterochaete andina* (FH), the genus type of *Heterochaete*. The phylogenetic analyses show highly supported sister-taxa relationships of *H.*

andina and *E. effusa* while other *Exidiopsis* species included in the analysis are more distantly related.

(G) *Exidiopsis griseobrunnea* clade is represented by a single species which is, according to our data, not related to the generic type of *Exidiopsis*, *E. effusa*. A new genus, *Sclerotrema*, is introduced for *E. griseobrunnea*.

ITS phylogeny. The final nrITS alignment contained 592 characters (including gaps). The overall topologies of the ML and BI trees were almost congruent. Most clades recovered were strongly supported in both analyses. The ML resulting ITS tree is presented in Fig. 2.

The phylogenetic tree indicates an existence of 15 divergent lineages or phylogenetic taxa within the group of species involved into analyses. Almost all species-level clades received rather high or 100% support in all analyses. The *Eichleriella leucophaea* lineage is not strongly supported. However, the specimens (LE 303261, *Larsson 15277, 15299*) belonging to this lineage are characterized by identical morphological features what allows us to treat them as a single taxon with sufficiently high intraspecific ITS variability (2.4–3%).

The phylogenetic concepts of *E. sicca*, *E. flavida* and *E. macrospora* remain uncertain due to low molecular differences between them (with percentage of genetic divergence in their nrITS sequences < 2%) and scarcity of sequenced collections. However, their morphological differences are significant and thus prevent considering them one species.

Two different datasets (nrITS and nrITS + nrLSU) and topologies derived from them are not in conflict with each other nor are they with morphological data. The phylogenetic analyses confirmed the heterogeneity of the *Auriculariales* with stereoid basidiocarps and demonstrated that *Eichleriella* in the traditional sense is a polyphyletic taxon comprising several, only distantly related genera.

3.2. Morphological data

In older literature, the basidiocarp form (effused or effused-reflexed to pileate, with adnate or free margin) and its ability to perennial growth were the main grounds for dividing species between *Eichleriella* and *Exidiopsis* (Lowy 1971, Wells and Raitviir 1980), while a presence of sterile spines on hymenial surface was the only reason to place the species to *Heterochaete* (Bodman 1952, Reid 1970). Our study shows that these characters are meaningful for the species recognition only, not for defining genera.

Among anatomical features, hyphal structure and basidial shape / size are of the utmost value at both generic and species levels. Hyphal structures were poorly studied in the *Auriculariales*, except a few poroid genera (Miettinen et al. 2012, Sotome et al. 2014). Only Bodman (1952) and Roberts (2006, 2008) paid attention to the presence of skeletal hyphae in some *Heterochaete* spp. From four genera treated below in detail, *Sclerotrema* contains one monomitic species, while *Amphistereum* embraces two truly dimitic species. All species of *Eichleriella* s.str. are monomitic (with one exception), with more or less clearly differentiated subicular hyphae. *Heteroradulum*, as defined here, encompasses two monomitic and five dimitic species. In the latter ones, clear transitions occur between more or less thin-walled generative to thick-walled, fibrous, often irregularly inflated and moderately cyanophilous skeletal hyphae.

Heteroradulum spp. are also characterized by peculiar basidia; they have a distinct basal segment, the so-called 'enucleate stalk', separated from four apical cells gradually tapering to thick sterigmata. In other genera mentioned here basidia are ellipsoid-ovoid, with conventionally looking, rather slender sterigmata, and they produce a strongly reduced, poorly visible enucleate stalk only in exceptional cases. Most species dealt with below possess sterile hymenial cells – hymenial cystidia ('paraphyses' in terms of Wells & Raitviir 1980); in a few cases, they are important for the species identification. Basidiospores of *Eichleriella* spp. are cylindrical to allantoid, straight or slightly curved, thin-walled, similar to many other representatives of the order; in *Heteroradulum* they bear a characteristic, blunt apiculus.

4. Taxonomy

4.1. *Amphistereum* Spirin & V. Malysheva, gen. nov.

MB 818018

Etymology. 'amphi-' (Greek, prefix) – both ways, and *Stereum*, a genus of basidiomycetes; the name implies a high macroscopic similarity to other stereoid fungi.

Basidiocarps annual or perennial, cupulate-orbicular, hard leathery. Hymenophore smooth, pale coloured. Hyphal structure dimitic; skeletal hyphae coloured (pale to dark brown), non-branching and located in the uppermost part of context or richly dichotomously branching and then dominating in the whole basidiocarps; generative hyphae clamped. Cystidia rare, thin-walled. Basidia ellipsoid-ovoid, longitudinally septate, four-celled, embedded; no enucleate stalk. Basidiospores hyaline, cylindrical to thick cylindrical, slightly curved, with accidental oily inclusions. On dry, still attached or fallen branches of deciduous trees.

Type. *Eichleriella schrenkii* Burt.

The genus embraces two species with sturdy, dimitic basidiocarps. Richly branched skeletal hyphae are dominating in all parts of the *A. leveilleanum* basidiocarps. In *A. schrenkii* vegetative hyphae occur exclusively in the uppermost parts of the context, and they look like normal skeletal hyphae. Pronounced dimitic structure and smooth hymenium surface differ *Amphistereum* from *Eichleriella* (the sole dimitic representative of the latter genus, *E. tenuicula*, has spiny hymenophore) while ellipsoid-ovoid basidia make it distinuishable from *Heteroradulum*.

4.1.1. *Amphistereum leveilleanum* (Berk. & M.A. Curtis) Spirin & V. Malysheva, comb. nov. – Fig. 3, 13.

≡ *Corticium leveilleanum* Berk. & M.A. Curtis, Hooker's J. Bot. 1: 238, 1849.

MB 818020

Basidiocarps perennial, cupulate-orbicular, hard leathery, up to 3 cm in widest dimension and up to 1 mm thick. Margin partly detaching, sometimes involute; abhymenial surface pink to pale ochraceous, azonate, even. Hymenophore hard leathery, first smooth, pink to ochraceous-orange, in fertile areas delicately pruinose, then fading to pale ochraceous or pale grey, in oldest basidiocarps concentrically sulcate.

Hyphal structure dimitic; hyphae with clamp connections. Skeletal hyphae dominating, pale brown, thick-walled, dichotomously branching, subparallel to interwoven in subicular part, densely interwoven in trama, central axes 3–6 μm in diam., terminal branches 1.5–2.5 μm in diam., CB (+). Generative hyphae scarce, hyaline, thin- or slightly thick-walled, 3–4 μm in diam. Cystidia rare, ventricose, apically blunt, 13–15 × 6.5–7.5 μm. Basidia ellipsoid-ovoid, four-celled, 13.3–17.8 × 8.7–10.6 μm (n = 10/1). Basidiospores cylindrical, slightly curved, 12–16 × 5–6 μm (fide Burt 1915: 745).

Notes. *Amphistereum leveilleanum* is a distinct species due to tough, stereoid, bright-coloured basidiocarps composed mostly by richly branched skeletal hyphae. Unfortunately, specimens studied by us are almost sterile: a few basidiospores seen are within the variation range given by Burt (1915) and Wells (1961). The species was reported from North and South America, from dead branches of deciduous trees (Burt 1915, Lowy 1971, Wells 1961).

Specimens examined. USA. Mississippi: Washington Co., Stoneville, *Carya aquatica* (?), 7.X.1955 *Lentz** (CFMR FP-106715). South Carolina, *Quercus* sp., comm. *Ravenel* (Fungi Caroliniani Exsiccati 2: 35, 1853) (H).

4.1.2. *Amphistereum schrenkii* (Burt) Spirin & V. Malysheva, comb. nov. – Fig. 4, 13, 15.

≡ *Eichleriella schrenkii* Burt, Ann. Missouri Bot. Garden 2: 744, 1915.

MB 818019

Basidiocarps annual, cupulate-orbicular, leathery, up to 0.3 cm in widest dimension and up to 0.5 mm thick. Margin elevated, sometimes involute; abhymenial surface pale brown, azonate, densely hirsute. Hymenophore soft ceraceous, smooth, white to pale grey.

Hyphal structure dimitic; hyphae with clamp connections. Hyphae of abhymenial surface pale brown, thick walled, occasionally clamped, loosely arranged, subparallel, 4–6 μm in diam., CB (+), with accidental crystals. Skeletal hyphae pale to dark brown, very thick-walled, arranged in parallel bundles, often densely glued together, present in the uppermost part of context and producing more or less solid layer (visible under ×50 magnification as a dark brown line), 2–4 μm in diam., CB (+). Generative hyphae hyaline, with distinct walls, dominating in upper trama, interwoven and partly glued together, (2.2–) 2.4–4.2 (–5.2) μm in diam. (n = 20/1), CB (+), sometimes encrusted by scattered angular crystals. Subhymenial hyphae hyaline, thin- or slightly thick-walled, short-celled, vertically arranged, 2–4 μm in diam., occasionally inflated up to 6 μm. Cystidia rather rare, narrowly clavate, some slightly tapering to the apex or indistinctly constricted, 31–49 × 5–7 μm. Hyphidia abundant, covering hymenial surface, richly branched, 2–3 μm in diam. at the apex. Basidia ellipsoid-ovoid, four-celled, (15.2–) 17.8–31.2 (–35.3) × (9.8–) 10.0–13.5 (–14.0) μm (n = 20/1). Basidiospores broadly cylindrical, slightly curved, (11.0–) 11.8–14.3 (–15.0) × (5.9–) 6.0–7.1 (–7.2) μm (n = 30/1), L = 13.12, W = 6.51, Q = 2.02.

Notes. *Amphistereum schrenkii* produces small-sized, cup-like basidiocarps with a pale-coloured hymenial surface. Its distribution is limited to arid regions of the US South-West (Arizona, New Mexico, Texas), where it occurs mostly on dead branches of mesquite (*Prosopis* spp.) (Burt 1915, Gilbertson et al. 1976 – as '*Exidiopsis leucophaea*', Wells & Raitviir 1980).

Specimen examined. USA. Arizona: Pima Co., Coronado Nat. Forest, *Prosopis juliflora*, 8.IX.1975 *Burdsall 8476** (CFMR).

4.2. *Eichleriella* Bres., Ann. Mycol. 1: 115, 1903.

Basidiocarps annual or short-living perennial, cupulate or resupinate, orbicular, in some species fusing together, soft leathery to ceraceous. Hymenophore smooth, pale coloured, in some species covered by sterile spines. Hyphal structure monomitic (except one dimitic species), hyphae clamped, often coloured in subiculum. Cystidia / gloeocystidia often present. Basidia ellipsoid-ovoid, longitudinally septate, 2- or 4-celled, embedded; without or rarely with a strongly reduced enucleate stalk. Basidiospores hyaline, cylindrical to narrowly cylindrical, distinctly curved, with accidental oily inclusions. On dry, still attached or fallen branches of deciduous trees.

Lectotype. *Eichleriella incarnata* Bres. (selected by Burt 1915: 743).

This genus was introduced by Bresadola (1903) with two new species, *E. incarnata* and *E. leucophaea*, described on the same page. Burt (1915) mechanically selected the first species as the genus type. Wells (1961) stated that *E. incarnata* represents the same species with *E. alliciens* originally described from Brazil, and placed the former species to the synonyms of the latter one. After studying type material of *E. alliciens*, *E. incarnata* and *E. leucophaea*, we came to another conclusion. *Eichleriella alliciens* sensu typi is the American species with soft and totally resupinate basidiocarps, while types of *E. incarnata* and *E. leucophaea* possess no essential differences from each other and belong to the same species with cupulate, rather tough fruitbodies. DNA sequences of recent collections from North America and Europe confirm our viewpoint. Here we place *E. incarnata* to the synonyms of *E. leucophaea* because the latter name already persists in mycological literature for a hundred years, and changing it to the completely forgotten *E. incarnata* is undesirable.

As re-defined here, the genus includes ten species closely related to *E. leucophaea*. All but one species are monomitic, often with slightly or distinctly thick-walled and brownish subicular hyphae. Hyphal structure differentiates *Eichleriella* from *Amphistereum* spp. which are otherwise morphologically very similar. According to DNA data, three species formerly addressed to the genus *Heterochaete* (*H. flavida, H. shearii* and *H. tenuicula*) belong to *Eichleriella*. They all have two-celled basidia while the rest of *Eichleriella* species normally bear four-celled ones. One of these species, *H. tenuicula*, is dimitic.

4.2.1. *Eichleriella alliciens* (Berk. & Cooke) Burt, Ann. Missouri Bot. Garden 2: 746, 1915. – Fig. 5, 14, 15.

≡ *Stereum alliciens* Berk. & Cooke, Bot. J. Linnean Soc. 15: 389, 1877.
Lectotype. Brazil. Minas Gerais: São Antonio da Boa Vista, Rio Javary, ‘on stick’, *Phillips* (K, studied) (selected by Burt 1915: 746).

= *Eichleriella mexicana* Burt, Ann. Missouri Bot. Garden 13: 334, 1926.
Holotype. Mexico. Morelos: Cuernavaca, Tepeite Valley, ‘on bark of a decaying frondose limb’, 28.XII.1909 *Murrill 399* (NY, studied).

Basidiocarps annual or short-living perennial, resupinate, first orbicular, later fusing together, soft leathery, up to 5 cm in widest dimension and up to 0.3 mm thick. Margin partly detaching, concolorous with or slightly paler than hymenial surface. Hymenophore soft leathery, smooth, pinkish to pale ochraceous, in older basidiocarps accidentally rimose and fading to pale ochraceous-grey.

Hyphal structure monomitic; hyphae with clamp connections. Subicular hyphae brownish, thick-walled, with a wide lumen, subparallel to interwoven, 2–4 μm in diam., CB (+), intermixed with thin-walled, hyaline hyphae. Tramal / subhymenial hyphae hyaline, thin- to slightly thick-walled, interwoven, partly glued together, (2.2–) 2.3–4.3 (–4.4) μm in diam. (n = 40/2), CB (+). Cystidia abundant, clavate or tubular, often sinuous, rarely tapering, 20–60 × 5–10 μm. Hyphidia abundant, covering hymenial surface, richly branched, 1–2.5 μm in diam. at the apex. Basidia ellipsoid-ovoid to subglobose, four-celled, (12.8–) 13.2–22.7 (–23.0) × (9.2–) 9.3–13.4 (–13.6) μm (n = 70/4). Basidiospores broadly cylindrical, slightly curved, (10.2–) 10.3–15.6 (–15.8) × (4.8–) 4.9–6.3 (–6.4) μm (n = 90/3), L = 12.37, W = 5.57, Q = 2.20–2.27. Crystals amorphous, scattered among hyphal tissues, up 10 μm in widest dimension.

Notes. *Eichleriella alliciens* was originally decribed from Brazil (Berkeley & Cooke 1877) and later reported from the Caribbean (Burt 1915) and the US South-East (Wells 1961). We compared the lectotype specimen and recent collections of *E. alliciens* from North America, and did not find any essential morphological differences between them. Therefore, we consider them conspecific. Morphologically, *E. alliciens* is most similar to the East Asian *E. crocata* which differs in having distinctly narrower basidiospores. The European records of *E. alliciens* treated by Wells (1961) refer to Eichler's collections of *E. incarnata* from Poland; in fact, they belong to *E. leucophaea* (see below).

Specimens examined. Brazil. Minas Gerais (lectotype). Rio Grande do Sul: Parecy Novo, 1924, VI.1928 *Rick* (NY), Santa Maria, 1936 *Rick* (NY), São Sebastião, III.1923 *Rick* (NY). São Paulo: São Paulo, Parque do Estado, 18.XII.1967 *Skvortzov* (NY). Cuba. Pinar del Río: San Diego de los Banos, on dead wood, 8–10.III.1905 *Earle & Murrill 296, 405* (NY). Guyana. Georgetown, Botanical Garden, on liana, 3.X.1923 *Linder 230* (NY). Jamaica. Castleton Gardens, 14–15.XII.1908 *Murrill 114* (NY). Mexico. Morelos (holotype of *E. mexicana*). USA. Florida: Dade Co., Long Pine Key, deciduous tree (branch), 17.VIII.1972 *Burdsall 7194** (CFMR), Matheson Hammock, *Coccolobis laurifolia* (dead branch), 1.XI.1942 *Singer* (NY). Mississippi: Washington Co., *Ilex decidua* (dead branches), 7.X.1955 *Lentz* (CFMR FP-106688). Venezuela. Vargas: Todasana, dead branches, 23.VII.1972 *Dumont VE-7352* (NY).

4.2.2. *Eichleriella bactriana* Spirin & V. Malysheva, sp. nov. – Fig. 13, 15.

Holotype. Turkmenistan. Kopet Dagh: Arvaz, *Berberis densiflora*, 16.X.1971 *Parmasto* (TAAM 55071).

MB 818021

Etymology. 'bactriana' (Lat., adj.) – from Bactria, a historical region in Middle Asia.

Basidiocarps annual or short-living perennial, cupulate-orbicular, leathery, up to 3 cm in widest dimension and up to 1 mm thick. Margin reflexed, often involute and undulate; abhymenial surface

ochraceous-brown to dark brown, azonate, uneven, adpressed-hispid. Hymenophore ceraceous, smooth or indistinctly plicate, pale grey, in older basidiocarps with pink hues.

Hyphal structure monomitic; hyphae with clamp connections. Subicular hyphae pale to dark brown, very thick-walled, arranged in dense parallel bundles, 3–4.5 μm in diam. Tramal hyphae hyaline, with irregularly thickened walls, interwoven, densely glued together, (2.2–) 2.3–3.9 (–4.2) μm in diam. (n = 20/1), CB (+), in the uppermost parts of trama torulose, 4–10 μm in diam., sometimes encrusted by scattered angular crystals. Subhymenial hyphae hyaline, thin- to slightly thick-walled, densely agglutinated, short-celled, 2–3.5 μm in diam. Cystidia rare, narrowly clavate, embedded, 25–32 × 5–6.5 μm. Hyphidia abundant, covering hymenial surface and in some portions producing continuous layer up to 40 μm thick, richly branched, 1–2 μm in diam. at the apex. Basidia ellipsoid-ovoid, four-celled, (17.8–) 18.0–24.8 (–25.3) × (11.3–) 12.0–13.9 (–14.2) μm (n = 30/2). Basidiospores cylindrical, slightly curved, (12.0–) 12.1–18.3 (–19.4) × (5.2–) 5.4–7.2 (–7.3) μm (n = 60/2), L = 14.76, W = 6.29, Q = 2.31–2.42.

Notes. *Eichleriella bactriana* is introduced here as a close relative of *E. leucophaea* from the Middle Asia. The main morphological differences between these species are thicker basidiocarps and wider basidiospores of *E. bactriana*.

Specimens examined. Tajikistan. Khatlon: Tigrovaya Balka Nat. Res., *Populus pruinosa*, 31.III.1977 *I. Parmasto** (TAAM 96698). Turkmenistan. Kopet Dagh: Arvaz (holotype), Dushak, *Colutea gracilis*, 29.X.1971 *Parmasto* (TAAM 55677, 55687); Kara-Kala, Ai-Dere, *Berberis* sp., 20.IV.1971 *Parmasto* (TAAM 54932). Uzbekistan. Tashkent: Chingan, *Berberis oblonga*, 25.IV.1982 *Parmasto** (TAAM 104431).

4.2.3. *Eichleriella crocata* (Pat.) Spirin & V. Malysheva, comb. nov. – Fig. 6, 13, 16.

≡ *Hirneolina crocata* Pat., Bull Soc. Mycol. France 40: 31, 1924.
Lectotype. Vietnam. Hanoi, 1921, *Petelot 45* (FH).

MB 818022

Basidiocarps annual or short-living perennial, resupinate, first orbicular, later fusing together, leathery, up to 2 cm in widest dimension and up to 0.3 mm thick. Margin partly detaching, concolorous with or slightly paler than hymenial surface. Hymenophore soft leathery, smooth, pale ochraceous, in older basidiocarps accidentally rimose and fading to pale grey.

Hyphal structure monomitic; hyphae with clamp connections. Subicular hyphae brownish, thick-walled, with a wide lumen, subparallel to interwoven, 2–4 μm in diam., CB (+). Tramal / subhymenial hyphae hyaline, with distinct walls, interwoven, freely spaced, mostly not glued together, (2.1–) 2.2–3.2 (–3.3) μm in diam. (n = 20/1), CB (+). Cystidia abundant, clavate, often sinuous, 23–39 × 4.5–10.5 μm. Hyphidia abundant, covering hymenial surface, richly branched, 2–2.5 μm in diam. at the apex. Basidia ellipsoid-ovoid, four-celled, (16.1–) 16.2–20.4 (–20.6) × (8.4–) 8.7–11.0 (–11.3) μm (n = 20/1). Basidiospores cylindrical, slightly or distinctly curved, (10.2–) 10.3–15.8 (–16.3) × (3.9–) 4.0–5.0 (–5.1) μm (n = 30/1), L = 13.41, W = 4.46, Q = 3.01.

Notes. *Eicheriella crocata* is reinstated here as the East Asian relative of *E. alliciens*. Both species are very similar macroscopically and differ from each other primarily by the basidiospore size and shape. *Eichleriella crocata* inhabits dead, still attached and recently fallen branches of angiosperms.

Specimens examined. Russia. Khabarovsk Reg.: Komsomolsk Dist., Selikhino, deciduous tree (fallen branch), 30.VIII.1961 *Parmasto* (TAAM 15526). Primorie Reg.: Kavalerovo Dist., Khrustalnyi, *Acer mono*, 4.X.1977 *Parmasto** (TAAM 101077); Lazo Dist., Lazo Nat. Res., *Acer* sp., 10.VIII.1986 *Parmasto** (TAAM 125909). Vietnam. Hanoi (lectotype).

4.2.4. *Eichleriella desertorum* Spirin & V. Malysheva, sp. nov. – Fig. 14, 16.

Holotype. Namibia. Otjozondjupa: Otjiwarongo, hardwood, 19.I.2014 *Ryvarden 49350** (O).

MB 818023

Etymology. 'desertorum' (Lat., adj.) – inhabiting arid areas.

Basidiocarps short-living perennial, resupinate, first orbicular, later fusing together, leathery, up to 5 cm in widest dimension and up to 0.2 mm thick. Margin compact, partly detaching, concolorous with hymenial surface. Hymenophore ceraceous, smooth and greyish-white.

Hyphal structure monomitic; hyphae with clamp connections. Subicular hyphae yellowish, slightly thick-walled, subparallel to interwoven, partly glued together, 2.5–4 μm in diam., CB–. Tramal / subhymenial hyphae hyaline, thin-walled or with distinct walls, interwoven, partly glued together, (2.2–) 2.3–3.8 (–4.2) μm in diam. (n = 20/1), CB–. Cystidia occasionally present, 20–41 × 5–7 μm. Hyphidia abundant, covering hymenial surface, richly branched, 0.5–1 μm in diam. at the apex. Basidia broadly ellipsoid-ovoid, four-celled, (15.2–) 15.6–18.8 (–19.1) × (12.3–) 12.8–14.7 (–15.0) μm (n = 20/2), some with a strongly reduced enucleate stalk. Basidiospores cylindrical, distinctly curved, (12.0–) 12.3–17.3 (–18.0) × (5.0–) 5.2–7.0 (–7.2) μm (n = 60/2), L = 14.53, W = 6.07, Q = 2.37–2.45.

Notes. *Eichleriella desertorum* is morphologically most similar to the North American *E. macrospora* and *E. sicca*. It is described here based on DNA data and different geographic distribution.

Specimens examined. Namibia. Otjozondjupa: Otjiwarongo (holotype), Waterberg Lodge, hardwood, 20.I.2014 *Ryvarden 49386* (O).

4.2.5. *Eichleriella flavida* (Pat.) Spirin & V. Malysheva, comb. nov. – Fig. 7, 14, 16.

≡ *Heterochaete flavida* Pat., Bull. Soc. Mycol. France 28: 31, 1912.
Lectotype. Guinea: Conakry, Camayenne, fallen branches, 8.VII (year not indicated) *Duport 90* (FH, studied) (selected by Bodman 1952: 207).

MB 818024

Basidiocarps annual, resupinate, orbicular, leathery, covering several cm and up to 0.15 mm thick. Margin adnate, first pruinose, later more or less compact, concolorous with or slightly paler than hymenial surface. Hymenophore leathery, first smooth or indistinctly tuberculate, then covered by sharp-pointed sterile spines 0.03–0.06 mm long, 6–7 per mm, pale grey to light ochraceous-grey, senescent basidiocarps fading to almost white.

Hyphal structure monomitic; hyphae with clamp connections. Subicular hyphae brownish, with slightly or distinctly thickened walls, in subparallel bundles, densely arranged, 2.5–4 μm in diam., CB (+). Tramal hyphae hyaline, thin-walled, densely interwoven, (2.0–) 2.1–3.2 (–3.4) μm in diam. (n = 20/1), CB (+), in spines brownish, with distinctly thickened walls, more or less vertically and tightly arranged, 2.5–4 μm in diam.; subhymenial hyphae similar to tramal ones, thin-walled. Cystidia abundant, clavate to fusiform, 26–52 × 7–11 μm, some with refractive, CB (+) content (gloeocystidia). Hyphidia abundant, covering hymenial surface, richly branched, 2.5–4 μm in diam. at the apex. Basidia ellipsoid-ovoid, predominantly two-celled, in exceptional cases four-celled, (10.3–) 11.3–15.3 (–16.8) × (8.1–) 8.5–11.3 (–11.6) μm (n = 30/2), rarely with a strongly reduced enucleate stalk. Basidiospores cylindrical, slightly to distincly curved, (10.8–) 11.2–16.1 (–16.2) × (5.0–) 5.1–6.5 (–7.4) μm (n = 90/3), L = 13.16, W = 5.73, Q = 2.20–2.44.

Notes. Bodman (1952) placed *Heterochaete flavida* to the synonyms of *H. andina*. We re-studied their type specimens and found that they represent two different species. *Heterochaete flavida* possesses two-celled basidia and its basidiospores are clearly wider than those of *H. andina*. Four recent collections from St. Helena, Zambia and Zimbabwe are morphologically identical to the type specimen of *H. flavida*, and we consider them conspecific. *H. flavida* is strongly reminiscent of the North American *H. shearii* which differs in having thicker basidiocarps, longer spines and detaching margin. According to DNA data, both *H. flavida* and *H. shearii* belong to *Eichleriella* and, therefore, they are transferred to this genus.

Specimens examined. Guinea: Conakry (lectotype). St. Helena. The Boers Graveyard, hardwood, 1.II.2014 *Ryvarden 49412** (K, H), Scotland Agriculture Station, hardwood, 3.II.2014 *Ryvarden 49469* (K, H). Zambia. Central Territory: Mukushi, corticated hardwood log, 12.II.2013 *Kotiranta 26007* (H). Zimbabwe. Matabeleland: Victoria Falls, hardwood, 28.I.1992 *Ryvarden 31497* (H ex O).

4.2.6. *Eichleriella leucophaea* Bres., Ann. Mycol. 1: 116, 1903. – Fig. 14, 15.

Lectotype. Poland. Podlaskie Reg., *Carpinus betulus* (fallen branch), XI.1900 *Eichler 19* (herb. Bresadola #19, S F20278, studied) (selected by Wells 1961: 353).

= *Eichleriella incarnata* Bres., Ann. Mycol. 1: 116, 1903.
Syntypes. Poland. Podlaskie Reg., *Berberis vulgaris* (fallen branch), I.1901 *Eichler 4* (S F20252), deciduous tree (fallen branch), XI.1900 *Eichler 36* (S F20251, studied) (selected by Wells 1961: 355, as ‘paratypes’).

Basidiocarps annual or short-living perennial, cupulate-orbicular, leathery, up to 3 cm in widest dimension and up to 0.5 mm thick. Margin partly detaching, sometimes involute and undulate; abhymenial surface pale to dark brown, indistinctly to clearly zonate, uneven, hispid or covered by scattered small warts. Hymenophore soft ceraceous, smooth, pale cream coloured to pale grey, in older basidiocarps sometimes with reddish tints, in herbarium specimens often rather tough and with more or less pronounced vinaceous-brown stains.

Hyphal structure monomitic; hyphae with clamp connections. Subicular hyphae pale to dark brown, very thick-walled, arranged in parallel bundles and often densely glued together, 2.5–4 μm in diam., sometimes torulose and then 7–8 μm in diam. Tramal hyphae hyaline to very pale brown, with distinct and irregularly thickened walls, subparallel to interwoven, partly glued together, (2.0–) 2.2–

5.1 (–5.2) µm in diam. (n = 80/4), CB (+), in uppermost parts of trama torulose, 5–12 µm in diam., sometimes encrusted by scattered angular crystals. Subhymenial hyphae hyaline, thin- - to slightly thick-walled, short-celled, 2–5 µm in diam. Cystidia rare, clavate to bullet-shaped, 20–25 × 4.5–6 µm, or absent. Hyphidia abundant, covering hymenial surface and in some portions producing continuous layer up to 60 µm thick, richly branched, 0.5–1 µm in diam. at the apex. Basidia ellipsoid-ovoid, four-celled, (12.0–) 12.3–22.1 (–22.8) × (8.8–) 9.0–12.3 (–13.1) µm (n = 70/4), rarely with a strongly reduced enucleate stalk. Basidiospores narrowly cylindrical, distinctly curved, (12.2–) 12.5–20.0 (–21.3) × (4.2–) 4.4–6.1 (–6.2) µm (n = 110/4), L = 14.61, W = 5.14, Q = 2.66–3.27.

Notes. The type material of *E. leucophaea* has been illustrated in Prieto-García et al. (2010). *Eichleriella leucophaea* is morphologically most similar to the Middle Asian *E. bactriana*, and it differs in having thinner basidiocarps and narrower basidiospores. *E. leucophaea* is distributed in temperate zone of Europe, inhabiting still attached or recently fallen branches of deciduous trees.

Specimens examined. Austria. Niederösterreich: Mödling, Wienerwald, *Carpinus betulus* (fallen branches), II.1903 *Höhnel* (S F257468). France. Allier: St. Priest, *Crataegus*, 28.III.1906 *Bourdot 4599* (S F257470). Germany. Sachsen: Leipzig, *C. betulus* (fallen branches), 30.X.1867 herb. *Bresadola* (S F257465). Italy. Tuscany: Florence, Leccio, *Quercus ilex*, *Martelli* (S F257467). Poland. Podlaskie Reg. (S, syntypes of *E. incarnata* and lectotype of *E. leucophaea*); without collecting data, *Berberis vulgaris*, *Eichler* (S F257438). Russia. Kursk Reg.: Kursk Dist., Solovyatnik, *Padus avium*, 27.V.2001 *Barsukova** (LE 303261). Spain. Guadalajara: Tamajon, deciduous tree (fallen branches), 4.XI.2011 *Larsson 15277**, *15299** (O).

4.2.7. *Eichleriella macrospora* (Ellis & Everh.) Martin, Univ. Iowa Stud. Nat. Hist. 18 (3): 48, 1944. – Fig. 14, 16.

≡ *Corticium macrosporum* Ellis & Everh., Bull. Torrey Bot. Club 27: 49, 1900.
Lectotype. USA. Ohio, *Fraxinus* (?) (dead limbs), *Lloyd 3113* (NY 00776547) (selected by Wells 1961: 352).

Basidiocarps annual or short-living perennial, resupinate, first orbicular, later fusing together, leathery, up to 5 cm in widest dimension and up to 0.3 mm thick. Margin compact, partly detaching, concolorous with or slightly paler than hymenial surface. Hymenophore ceraceous, first smooth and greyish-white, later irregularly tuberculate and pale ochraceous.

Hyphal structure monomitic; hyphae with clamp connections. Subicular hyphae almost hyaline to pale brown, slightly thick-walled, subparallel, partly glued together, 2–4 µm in diam., CB (+). Tramal / subhymenial hyphae hyaline, thin-walled or with distinct walls, interwoven, partly glued together, (2.0–) 2.1–3.8 (–4.5) µm in diam. (n = 40/2), CB (+). Cystidia abundant, clavate, often sinuous, 21.5–63 × 4–9 µm, with accidental lateral outgrowths. Hyphidia abundant, covering hymenial surface, richly branched, 1.5–3 µm in diam. at the apex. Basidia ellipsoid-ovoid, four-celled, (15.0–) 15.2–24.7 (–25.2) × (10.5–) 10.6–12.2 (–12.6) µm (n = 40/2). Basidiospores cylindrical to broadly cylindrical, distinctly curved, (12.2–) 12.3–16.5 (–16.7) × (5.3–) 5.6–7.1 (–7.3) µm (n = 80/3), L = 13.63, W = 6.20, Q = 2.04–2.41.

Notes. *Eichleriella macrospora* is a characteristic species due to orbicular, greyish basidiocarps with sharply delimited, partly detaching margins. The species is distributed in temperate forests of the US North-East and found on dead, still attached or recently fallen branches of deciduous trees.

Specimens examined. USA. Iowa: Dickinson Co., Okoboji, fallen branches, 4.VIII.1933 *Martin 1316* (NY), 23.VIII.1933 *Rogers 334* (NY); Welch Lake, *Fraxinus* sp. (fallen branches), 9.VIII.1933 *Martin* (NY); Johnson Co., Iowa City, *Acer negundo*, 15.IX.1940 *Martin* (NY), 14.IX.1941 *Martin* (TENN). Ohio (lectotype). Texas: Austin, Zilker Park, *Ulmus rubra* (?), 15.VIII.2013 *Miettinen 16683.2* (H). Wisconsin: La Crosse Co., Coon Valley, *A. negundo* (dead branches), 21.IX.1979 *Nakasone** (CFMR FP-101769).

4.2.8. *Eichleriella shearii* (Burt) Spirin & V. Malysheva, comb. nov. – Fig. 14, 16.

≡ *Sebacina shearii* Burt, Ann. Missouri Bot. Garden 2: 758, 1915.

MB 818025

Basidiocarps annual, orbicular, leathery, covering several cm and up to 0.2 mm thick. Margin compact, first adnate, then detaching, concolorous with or slightly paler than hymenial surface. Hymenophore leathery, first smooth or indistinctly tuberculate, then covered by sharp-pointed sterile spines 0.05–0.2 mm long, 6–7 per mm, pale grey to light ochraceous-grey, in older basidiocarps fading to almost white.

Hyphal structure monomitic; hyphae with clamp connections. Subicular hyphae brownish, with slightly or distinctly thickened walls, in subparallel bundles, densely arranged, 3–4.5 μm in diam., CB (+). Tramal hyphae hyaline, thin- or slightly thick-walled, densely interwoven, (2.5–) 2.7–3.8 (–4.0) μm in diam. (n = 20/1), CB (+), in spines brownish, with distinctly thickened walls, more or less vertically and tightly arranged, 2.5–4 μm in diam., in apical parts of spines often bearing large crystal agglomerations up to 25 μm in diam.; subhymenial hyphae similar to tramal ones, thin-walled. Cystidia abundant, clavate to fusiform, 20–40 × 5–9 μm, some with refractive, CB (+) content (gloeocystidia). Hyphidia abundant, covering hymenial surface, richly branched, 1–2 μm in diam. at the apex. Basidia ellipsoid-ovoid, predominantly two-celled, (11.3–) 11.8–15.8 (–16.3) × (8.0–) 8.2–10.3 (–11.0) μm (n = 20/2), rarely with a strongly reduced enucleate stalk. Basidiospores cylindrical, distinctly curved, (10.3–) 11.4–16.2 (–16.3) × (5.0–) 5.1–7.1 (–7.6) μm (n = 90/3), L = 13.76, W = 6.01, Q = 2.13–2.39.

Notes. *Eichleriella shearii* is the North-American counterpart of *E. flavida*. See remarks to the latter species. Dueñas (2005) reported it from Spain, and here we report it also from France.

Specimens examined. France. Pyrénées-Orientales: Argelès-sur-Mer, hardwood (dry branches), 2.XI.2008 *Larsson 13785** (GB, H). Mexico. Vera Cruz: Xalapa, Botanical Garden, hardwood, 22.IX.1985 *Ryvarden 23258*, 23308* (O). USA. Florida: Alachua Co., Gainesville, *Vitis* sp., 14.II.1944 *Murrill* (NY).

4.2.9. *Eichleriella sicca* Spirin & Miettinen, sp. nov. – Fig. 14, 16.

Holotype. USA. Arkansas: Van Buren Co., Clinton, fallen branches of *Acer negundo*, 22.X.2013 *Miettinen 17349** (H).

MB 818026

Etymology. ‘siccus’ (Lat., adj.) – dry, arid.

Basidiocarps annual, resupinate, first indeterminable, later fusing together and more or less clearly orbicular, soft ceraceous, up to 2 cm in widest dimension and up to 0.1 mm thick. Margin first pruinose, then compact, adnate, concolorous with hymenial surface. Hymenophore soft ceraceous, smooth, white to pale cream-coloured, in oldest parts irregularly rimose.

Hyphal structure monomitic; hyphae with clamp connections. Subicular hyphae hyaline, thin-walled, subparallel, 2–4 μm in diam., CB (+). Tramal / subhymenial hyphae hyaline, thin-walled, loosely interwoven, (2.1–) 2.2–3.3 (–3.8) μm in diam. (n = 20/1), CB (+). Cystidia absent. Hyphidia abundant, loosely arranged, covering hymenial surface, richly branched, 1.5–2.5 μm in diam. at the apex. Basidia ellipsoid-ovoid, four-celled, (16.1–) 16.2–22.8 (–23.2) × (9.3–) 9.5–11.8 (–12.3) μm (n = 20/1), sometimes with a reduced enucleate stalk. Basidiospores cylindrical, distinctly curved, (10.9–) 11.3–14.6 (–15.3) × (5.2–) 5.3–6.3 (–7.2) μm (n = 30/1), L = 12.83, W = 5.77, Q = 2.23.

Notes. *Eichleriella sicca* is morphological close to *E. desertorum* and *E. macrospora*. The latter species possesses well-developed and abundant cystidia, longer basidiospores and thicker basidiocarps with partly detaching margin. So far *E. sicca* is known from the type locality.

4.2.10. *Eichleriella tenuicula* (Durieu & Lév.) Spirin & V. Malysheva, comb. nov. – Fig. 14.

≡ *Hydnum tenuiculum* Durieu & Lév., Ann. Sci. Nat., Bot., sér. 3, 5: 145, 1846.
Lectotype. Indonesia. Java: Tjikoya, I.1843 *Zollinger 1078B* (PC 0706782) (selected here).

= *Heterochaete leveillei* Pat., Bull. Soc. Mycol. France 10: 75, 1894.
Lectotype. Indonesia. Java: Tjikoya, I.1843 *Zollinger 1078A* (FH, duplicate PC 0706781 – studied) (selected by Bodman 1952: 217).
MB 818027

Spiny hymenium and two-celled basidia of *E. tenuicula* are reminiscent of *E. flavida* and *E. shearii*. However, basidiocarps of *E. tenuicula* are composed mostly by brownish, thick-walled skeletal hyphae; at the present moment, it is the only dimitic species known in the genus *Eichleriella*. Modern description of this species is given by Roberts (2008) (as *Heterochaete tenuicula*).

Specimens examined. Indonesia. (lectotypes of *H. tenuiculum* and *H. leveillei*). Pakistan. Lahore, on dead branches, 7.IV.1950 *Ahmad* (H ex GZ). Thailand. Cangwat Chiang Mai, Amphoe Mae Rim, Kong Hae, hardwood, 15.II.1979 *Ryvarden 17599** (H ex O).

4.3. *Heteroradulum* Lloyd, gen. nov.

MB 818028

Basidiocarps annual or perennial, orbicular, often fusing together, in one species effused-reflexed, leathery. Hymenophore smooth, as a rule with pink or red tints, with occasional fertile outgrowths or covered by regularly arranged sterile spines. Hyphal structure mono- or dimitic, hyphae clamped, sometimes irregularly inflated, coloured in subiculum and trama. Cystidia / gloeocystidia present. Basidia narrowly ovoid to obconical, longitudinally septate, constantly four-celled, embedded, often with a well-developed enucleate stalk. Basidiospores hyaline, cylindrical to broadly cylindrical,

sometimes curved, with oily inclusions and thick, blunt apiculus. On dry branches and logs of deciduous trees.

Type. *Radulum kmetii* Bres.

The genus name *Heteroradulum* was introduced by Lloyd (1917) although invalidly (as 'McGinty' – see Stevenson & Cash 1936). While discussing this possible new genus, Lloyd mentioned *Radulum kmetii* as its single representative. In addition, he correctly noticed possible close connections of the latter species with *Radulum deglubens* and *R. spinulosum* – they both are treated here as members of *Heteroradulum*. Therefore, we decided to validate Lloyd's genus.

Morphologically, *Heteroradulum* is a well-defined genus. Tough basidiocarps, rather brightly coloured (pinkish or reddish) hymenium, irregularly inflated hyphae, and large, obconical basidia are the best hints for recognizing it. In two temperate – boreal species, *H. deglubens* and *H. kmetii*, hymenial surface remains smooth for a long time and obtains irregularly arranged, sharpened outgrowths only at late stages of the basidiocarp existence. In contrast, five warm temperate – tropical species of *Heteroradulum* have spiny, *Heterochaete*-like hymenophore.

4.3.1. *Heteroradulum adnatum* Spirin & V. Malysheva, sp. nov. – Fig. 8, 15.

Holotype. Mexico. Vera Cruz: Barranca de Pescado, deciduous branch, with *Botryodontia cirrhata*, 26.IX.1985 *Ryvarden 23453** (O, isotype – H).

MB 818030

Etymology. 'adnatus' (Lat., adj.) – adnate, firmly attached to the substrate.

Basidiocarps annual, first orbicular, later fusing together, leathery, covering several cm in widest dimension and up to 0.3 mm thick. Margin adnate, first white, later more or less concolorous with hymenial surface. Hymenophore soft ceraceous, covered by sharp-pointed spines 0.1–0.2 mm long, 5–6 per mm, pink, in older basidiocarps and herbarium specimens with more or less pronounced vinaceous-brown stains.

Hyphal structure monomitic; hyphae with clamp connections. Subicular hyphae hyaline, with thickened walls, interwoven, 3.5–5.5 μm in diam., CB (+), partly glued together, not encrusted. Tramal hyphae hyaline, slightly to distinctly thick-walled, interwoven, densely arranged, (2.0–) 2.1–3.1 (–3.2) μm in diam. (n = 20/1), CB (+), in spines distinctly thick-walled, vertically arranged, cemented by amorphous brownish matter, 3–4 μm in diam.; subhymenial hyphae similar. Cystidia abundant, clavate to fusiform, 26–95 × 4–10 μm, often with refractive content (gloeocystidia). Hyphidia abundant, scattered among hymenial cells, embedded, simple or sparsely branched, 1.5–2 μm in diam. at the apex. Basidia narrowly ovoid to obconical, four-celled, (17.2–) 17.3–21.8 (–23.0) × (8.8–) 9.2–11.3 (–12.0) μm (n = 20/1), some with enucleate stalk up to 10 × 4 μm. Basidiospores broadly cylindrical, straight or indistinctly curved, rarely somewhat fusiform (longest spores only), (11.3–) 11.4–14.2 (–14.6) × (5.0–) 5.2–7.2 (–7.3) μm (n = 30/1), L = 12.64, W = 6.30, Q = 2.02.

Notes. *Heteroradulum adnatum* is most similar to *H. spinulosum* but it differs from the latter one in having fertile spines, monomitic basidiocarps, and smaller basidia and basidiospores.

4.3.2. *Heteroradulum brasiliense* (Bodman) Spirin & V. Malysheva, comb. nov.

≡ *Heterochaete brasiliensis* Bodman, Lloydia 15: 210, 1952.
Holotype. Brazil. Rio Grande do Sul: Salvador, V.1942 *Rick* (NY – isotype, studied).

MB 818031

This species was described and illustrated by Bodman (1952), and it is so far known only from Brazil (Roberts 2006). Small basidia and basidiospores of *H. brasiliense* are reminiscent of *H. adnatum*, although they smaller in the first species, 13–20 × 7–9 μm and (8.2–) 8.3–10.6 (–11.5) × (4.2–) 4.3–5.8 (–6.1) μm (n = 20/1), L = 9.52, W = 4.95, Q = 1.94, respectively. Moreover, *H. brasiliense* possesses sterile spines on hymenial surface and has no cystidia. Dimitic hyphal structure, encrusted skeletal hyphae, obconical basidia with rather wide sterigmata and short but easily detectable enucleate stalk, and cylindrical basidiospores with thick and blunt apiculus clearly indicate that this species is a member of *Heteroradulum*.

4.3.3. *Heteroradulum deglubens* (Berk. & Broome) Spirin & V. Malysheva, comb. nov. – Fig. 9, 13, 15.

≡ *Radulum deglubens* Berk. & Broome, Ann. Mag. Nat. History 15: 32, 1875.
Lectotype. United Kingdom. Scotland: Moray, Forres, *Fraxinus excelsior*, 30.I.1874 *Keith* (K) (selected and illustrated by Wells & Raitviir 1980: 573–575).

MB 818032

Basidiocarps annual or short-living perennial, first orbicular, later fusing together, leathery, covering several cm in widest dimension and up to 0.5 mm thick. Margin adnate or rarely slightly lifted, first white, later more or less concolorous with hymenial surface. Hymenophore soft ceraceous, first smooth, greyish pink, in older basidiocarps with reddish tints and often covered by irregularly arranged spines up to 1 mm long, in herbarium specimens with more or less pronounced vinaceous-brown stains.

Hyphal structure monomitic; hyphae with clamp connections. Subicular hyphae hyaline, with thickened walls, interwoven to subparallel, (1.8–) 1.9–3.1 (–3.2) μm in diam. (n = 40/2), CB (+), encrusted by sparse granular crystals, intermixed with very thin-walled hyphae 1.5–2 μm in diam. Tramal hyphae hyaline, thin-walled, interwoven and often twisted, densely arranged, (1.8–) 2.1–3.8 (–4.0) μm in diam. (n = 20/1), CB (+), sometimes encrusted by scattered brownish globules; subhymenial hyphae similar. Cystidia abundant to rare, clavate or skittle-shaped, 31–44 × 5–6 μm. Hyphidia abundant, scattered among hymenial cells, embedded or slightly projecting, richly branched, 1.5–2.5 μm in diam. at the apex, often covered by brownish globules or small amorphous crystals. Basidia obconical, four-celled, (26.0–) 26.1–40.2 (–44.8) × (9.3–) 9.8–13.7 (–14.0) μm (n = 75/4), with enucleate stalk up to 17 × 5 μm. Basidiospores cylindrical, slightly or distinctly curved, (13.0–) 13.1–19.8 (–20.4) × (6.0–) 6.1–8.1 (–8.2) μm (n = 120/4), L = 16.79, W = 7.07, Q = 2.26–2.52.

Notes. For a long time, *H. deglubens* was mixed up with *H. kmetii* and *H. spinulosum*. Reid (1970) made the first attempt to split them apart and stated that the type collection of *Radulum spinulosum* belongs to a species with spiny hymenium and gloeocystidia. Therefore, it could not be conspecific

with *Radulum deglubens*; the latter species was combined to *Eichleriella* and *R. spinulosum* kept in *Heterochaete*. Wells & Raitviir (1980) accepted this solution and placed *Radulum kmetii* to the synonyms of *E. deglubens*. However, our results show that this synonymy is wrong because *R. kmetii* represents a good species, and both of these species, as well as *R. spinulosum*, belong to *Heteroradulum*. Morphological differences of *H. deglubens* and *H. kmetii* are listed below.

Heteroradulum deglubens is the European species, with a wide distribution stretching from the Mediterranean to the subarctic zone. It favours thin, dry, still attached branches of deciduous trees although some records come from still standing or recently fallen logs.

Specimens examined. Armenia. Lori: Vanadzor, *Fagus orientalis*, 18.IX.1962 *Parmasto* (TAAM 15183). Estonia. Hiiumaa: Saarnaki, *Prunus* sp., 25.IX.2007 *Kotiranta 21294* (H). Lääne: Hanila, *Corylus avellana*, 9.VII.2007 *Miettinen 11716* (H). Läänemaa: Puhtu, deciduous forest, *Corylus avellana*, 1.VI.1956 *Parmasto** (LE 225523). Pärnumaa: Orajõe, *Salix caprea*, 17.IX.1957 *Parmasto* (TAAM 5795). Finland. Ahvenanmaa: Geta, Snäckö, *Fraxinus excelsior*, 24.X.2001 *Kotiranta 19051* (H). Kittilän Lappi: Muonio, Pallas-Ounastunturi Nat. Park, *Sorbus aucuparia*, 1.IX.2004 *Niemelä 7783* (H). France. Vosges, *F. excelsior* (dry branches), 1903 *Galzin* (S F257435). Norway. Akershus: Asker, Stokkerelva at Åstaddammen, *Alnus incana*, 5.V.2016 *Spirin 10030* (H). Oslo, deciduous tree, I.1911 *Egeland* (S F257437). Oppland: Østre Toten, Hensvoll, hardwood, 20.V.1977 *Ryvarden* (O). Troms: Målselv, Dividalen Nat. Park, *Salix borealis*, 13.IX.1976 *Solheim 1864** (O). Russia. Bryansk Reg.: Suzemsky Dist., Bryansky Les Nat. Res., *Quercus robur*, 22.X.2012 *Volobuev** (LE 291951). Karachaevo-Cherkessia: Teberda, *Lonicera* sp., 25.IX.1968 *Parmasto* (TAAM 53292). Krasnodar Reg.: Slavyansk Dist., Krasnyi Les, deciduous tree (fallen branch), 28.IX.1966 *Parmasto* (TAAM 19755). Leningrad Reg.: Tikhvin Dist., Ur'ya, *Sorbus aucuparia*, 25.IX.2011 *Spirin 4654** (H). Yamalo-Nenets Reg.: Priuralskii Dist., Slantsevaya Mtn., *Sorbus* sp., 31.VII.1965 *Kazanceva** (TAAM 064782). Spain. Balearic Islands: Majorca, Escorca, *Quercus ilex*, 22.X.1984 *G.M. Jenssen* (O). Sweden. Upland: Bondkyrka, decaying branches of frondose trees, 04.XI.1935 and 16.X.1936 *Lundell** (LE 38182); Älvkarleby, *S. aucuparia*, 20.X.1949 *Lundell* (O).

4.3.4. *Heteroradulum kmetii* (Bres.) Spirin & V. Malysheva, comb. nov. – Fig. 10, 13, 15.

≡ *Radulum kmetii* Bres., Atti Ist. Reale Accad. Rovereto 3 (3): 102, 1897.
Lectotype. Slovakia. Banská Bystrica: Prenčov, Mt. Sytno, *Populus tremula*, *Kmet** (H, studied) (selected here).

MB 818029

Basidiocarps perennial, first completely resupinate, later with well-developed caps, leathery, up to 5 cm in widest dimension and up to 2 mm thick, often fusing together; pilei projecting up to 1 cm. Pileal margin rather sharp, sometimes involute, margin of resupinate parts adnate, later partly detaching, concolorous to or slightly paler than hymenial surface; abhymenial surface pale ochraceous to grey, distinctly zonate, uneven, hispid. Hymenophore leathery, first smooth, pinkish or reddish, in older basidiocarps fading to pinkish grey and sometimes covered by irregularly arranged spines up to 1 mm long, in herbarium specimens with more or less pronounced vinaceous-brown stains and usually irregularly rimose.

Hyphal structure dimitic; hyphae with clamp connections. Subicular hyphae brownish, very thick-walled, arranged in parallel bundles, 2–4 μm in diam. Tramal skeletal hyphae brownish, distinctly

thick-walled, interwoven in uppermost parts, more or less vertically oriented close to hymenial surface, densely arranged, (2.0–) 2.2–4.4 (–5.1) μm in diam. (n = 200/10), CB (+), sometimes irregularly inflated up to 6 μm, as a rule encrusted by solid grainy crystals; generative hyphae rather rare, hyaline, thin- to distinctly thick-walled, 2.5–4 μm in diam., but some inflated up to 5–6 μm. Skeletocystidia present as endings of tramal skeletal hyphae, especially abundant in senescent basidiocarps, ventricose or spindle-shaped to subglobose, very thick-walled, 4–20 μm in diam., sometimes proliferating with apical dendroid outgrowths. Cystidia rarely present, clavate to bottle-shaped, 27–40 × 4–7.5 μm. Hyphidia abundant, covering hymenial surface, richly branched, 1–3 μm in diam. at the apex, often encrusted by brownish matter. Basidia obconical, four-celled, (27.4–) 29.2–45.2 (–45.4) × (9.7–) 9.8–14.5 (–14.7) μm (n = 97/10), with enucleate stalk up to 17 × 6 μm. Basidiospores cylindrical to broadly cylindrical, distinctly curved, (14.1–) 14.3–22.3 (–24.9) × (5.8–) 6.0–9.2 (–9.7) μm (n = 420/14), L = 18.38, W =7.26, Q = 2.31–2.90.

Notes. *Heteroradulum kmetii* is a distinct species due to thick, perennial, effused-reflexed basidiocarps. However, its young basidiocarps are completely resupinate and thus they can be confused with *H. deglubens*. In this case, the microscopic study is necessary. The primary anatomical feature of *H. kmetii* is a dimitic structure: the whole basidiocarp contains abundant, thick-walled, irregularly inflated, brownish skeletal hyphae. In turn, *H. deglubens* is a monomitic species: thick-walled hyphae can be detected in subiculum only but they are clamped, evenly outlined (not inflated) and narrower than in *H. kmetii*. These species are also distinguishable due to a different construction of hymenium, composed by openly arranged basidia in *H. deglubens* and those ones embedded in a dense layer of hyphidia in *H. kmetii*. Basidiospores are highly variable in both species.

Heteroradulum kmetii is a holarctic species reported here from Europe, Siberia, Russian Far East and North America. Almost all specimens studied by us were collected from dry branches and logs of *Populus* and *Salix* spp. The species certainly prefers to open, dry habitats.

Specimens examined. Austria. Niederösterreich: Tulln an der Donau, *Populus nigra*, ‘m. Oct.’ *Rechinger** (H, LE ex W, Kryptogamae Exsiccatae #1807). Canada. Alberta: Edmonton, Louise McKinney Riverfront Park, *Populus alba*, 28.VII.2015 *Spirin 8978*, *8981** (H), Henrietta Louise Edwards Park, *P. alba*, 28.VII.2015 *Spirin 8988** (H); Yellowhead Co., William A. Switzer Provincial Park, *Populus tremuloides*, 24.VII.2015 *Spirin 8858** (H), Hinton, *P. tremuloides*, 24.VII.2015 *Spirin 8864** (H). Ontario: Ottawa, Fallowfield, *Populus* sp., 13.V.1954 *Speirs** (H ex DAOM 31292); Peel Co., Palgrave, *Populus* sp., *Salix* sp., 6.XI.1955 *Cain* (H, LE 38181* ex TRTC 31696, 31697); Thunder Bay Dist., Black Sturgeon Lake, *Populus* sp., 10.IX.1973 *Ginns 2529** (H ex DAOM 145605). Norway. Oppland: Nord Fron, Liadalane Nat. Res., *Populus tremula*, 12.IX.2016 *Spirin 11032* (O, H). Finnmark: Alta, Storvannet Nat. Res., *Salix nigricans*, 19.VIII.1992 *Ryvarden 31795** (O), *Salix* sp., 18.VIII.1993 *Ryvarden 33201** (O), Vassbotndalen Nat. Res., *S. nigricans*, 17.VIII.1993 *Ryvarden & Sivertsen** (O ex TRH), *Salix* sp., 16.VIII.2011 *Siversten* (O). Russia. Kemerovo Reg.: Novokuznetsk, *P. tremula*, 30.IX.1930 *Kravtzev W174* (PRM 673140). Khabarovsk Reg.: Khabarovsk Dist., Malyi Kukachan, *Populus maximowiczii*, 17.VIII.2012 *Spirin 5326** (H), 18.VIII.2012 *Spirin 5394* (H); Verkhnebureinskii Dist., Sidorka, *Salix udensis*, 24.VIII.2014 *Spirin 7967** (H). Krasnoyarsk Reg.: Mana Dist., Badzhei, *P. tremula*, 5.IX.1958 *Parmasto** (TAAM 9847). Primorie Reg.: Krasnoarmeiskii Dist., Valinku, *Salix cardiophylla*, 28.VIII.2013 *Spirin 6466** (H); Shkotovo Dist., Anisimovka, *Populus* sp., 11.VIII.1991 *Govorova** (LE 303456); Ternei Dist., Sikhote-Alin Nat. Res., *P. tremula*, 12.IX.1987 *Kõljalg** (TAAM 149179). Slovakia. Banská Bystrica (lectotype). Ukraine. Luhansk Reg.: Slovianoserbsk Dist., Luhansk Nat. Res., *P. nigra*, 7.V.2011 *Ordynets* (CWU 5512, 6148, 6150, 6151, 6152*); Stanichno-Luhansky Dist., Luhansk Nat. Res., deciduous wood, 20.X.2010 *Akulov*

(CWU 4563*). USA. Minnesota: Clearwater Co., Itasca State Park, *Populus* sp. (?), 16.IX.1977 *Ryvarden 14358, 14389** (O).

4.3.5. *Heteroradulum lividofuscum* (Pat.) Spirin & V. Malysheva, comb. nov.

≡ *Heterochaete lividofusca* Pat., Bull. Soc. Mycol. France 9: 140, 1893.

MB 818033

Good description and illustrations of this species are given in Bodman (1952). Dimitic hyphal structure, abundant gloeocystidia, and large, obconical, 4-celled basidia with an enucleate stalk indicate that the species belongs to *Heteroradulum*. Basidiospores of *H. lividofuscum* are most similar to *H. kmetii*, (17.3–) 17.6–23.1 (–24.7) × (7.2–) 7.3–9.0 (–9.2) μm (n = 30/1), L = 20.55, W = 8.20, Q = 2.52. However, hymenial surface of *H. lividofuscum* is covered by densely arranged, sterile spines 6–7 per mm, and thus it is macroscopically reminiscent of *H. semis* and *H. spinulosum*.

Specimens examined. Ecuador. Quito, 1892 *Lagerheim 79* (NY, paratype). Jamaica. Blue Mts., St. Andrew Parish, on bark, 5.II.1949 *Van der Porten* (NY).

4.3.6. *Heteroradulum semis* Spirin & V. Malysheva, sp. nov. – Fig. 13, 15.

Holotype. China. Jilin: Antu Co., Huang Song Pu, *Acer* sp. (dead standing tree), 28.VIII.2005 *Miettinen 10618.1** (H).

MB 818034

Etymology. ‘semis’ (Lat., noun) – a small bronze coin in the Roman Republic; refers to small orbicular basidiocarps of the species.

Basidiocarps annual, orbicular, leathery, about 2 cm in widest dimension and up to 0.4 mm thick. Margin first adnate and white, compact, later slightly elevated and partly detaching, more or less concolorous with hymenial surface. Hymenophore leathery, covered by blunt-pointed spines 0.1–0.3 mm long, 5–7 per mm, pinkish ochraceous to pinkish grey, in older basidiocarps fading to greyish ochraceous.

Hyphal structure dimitic; hyphae with clamp connections. Subicular hyphae hyaline to brownish, very thick-walled, interwoven, 3–4 μm in diam. Tramal skeletal hyphae brownish, distinctly thick-walled, interwoven, densely arranged, (2.0–) 2.1–3.0 (–3.1) (n = 20/1), CB (+), often encrusted by densely arranged grainy crystals, in spines oriented, occasionally encrusted, in older parts cemented by amorphous brownish matter; generative hyphae hyaline, thin- to slightly thick-walled, 2–4 μm in diam. Cystidia uncommon, narrowly clavate, 37–43 × 4–5 μm. Hyphidia abundant, scattered among hymenial cells, embedded, simple or sparsely branched, 1.5–2 μm in diam. at the apex. Basidia narrowly ovoid to obconical, four-celled, (20.4–) 20.8–27.4 (–29.9) × (10.0–) 10.3–12.0 (–12.2) μm (n = 20/2), often with a short enucleate stalk up to 5 × 5 μm. Basidiospores broadly cylindrical to narrowly obovate, straight, (10.3–) 10.6–14.1 (–14.2) × (5.8–) 6.0–7.7 (–8.1) μm (n = 60/2), L = 11.83, W = 6.85, Q = 1.72–1.74.

Notes. *Heteroradulum semis* is similar to *H. lividofuscum* and *H. spinulosum* in having sterile, *Heterochaete*-like outgrowths on hymenial surface. The species is distributed in temperate forests of East Asia and reported here from China, Japan and South Korea.

Specimens examined. China. Jilin: Antu Co., Huang Song Pu (holotype), Erdao Bai He, hardwood, 26.VIII.2005 *Miettinen 10524.1* (H). Japan. Honshu: Ibaraki, Tsubaki Mt., hardwood, 7.XI.1991 *Ryvarden 30397* (H ex O).

4.3.7. *Heteroradulum spinulosum* (Berk. & M.A. Curtis) Spirin & V. Malysheva, comb. nov. – Fig. 11, 16.

≡ *Radulum spinulosum* Berk. & M.A. Curtis, Grevillea 1 (10): 146, 1873.
Lectotype. USA. Alabama, *Cephalanthus occidentalis*, *Peters 4543* (K, studied) (selected by Reid 1957: 129).

≡ *Heterochaete crassa* Bodman, Mycologia 41: 531, 1949.
Holotype. USA. Florida: Dade Co., Miami, Simpson Park, *Nectandra coriacea*, 17.XI.1942 *Singer* (NY, studied).

MB 818035

Basidiocarps annual, orbicular, leathery, about 1 cm in widest dimension and up to 0.3 mm thick. Margin adnate or slightly elevated, tomentose, first white or pale cream-coloured, later more or less concolorous with hymenial surface. Hymenophore soft ceraceous, covered by sharp-pointed spines 0.1–0.2 mm long, 6–7 per mm, bright ochraceous to pinkish grey, in some parts with more or less pronounced vinaceous-brown flecks.

Hyphal structure dimitic; hyphae with clamp connections. Subicular hyphae hyaline to brownish, very thick-walled, interwoven to subparallel, 4–6 μm in diam. Tramal skeletal hyphae hyaline to brownish, distinctly thick-walled, interwoven, densely arranged, (2.0–) 2.1–3.5 (–3.8) (n = 40/2), some hyphae accidentally inflated up to 5 μm in diam., CB (+), often encrusted by scattered grainy crystals, in spines more or less vertically oriented and cemented by amorphous brownish matter; generative hyphae hyaline, thin- to slightly thick-walled, 2.5–4 μm in diam., but some inflated up to 5–6 μm. Skeletocystidia occasionally present as endings of tramal skeletal hyphae, ventricose or spindle-shaped, thick-walled, 5–6 μm in diam. Cystidia clavate to bottle-shaped, 23–45 × 6–7 μm, often with refractive content (gloeocystidia). Hyphidia abundant, scattered among hymenial cells, embedded or projecting up to 30 μm above basidia, simple or sparsely branched, 2–4 μm in diam. at the apex. Basidia narrowly ovoid to obconical, four-celled, (17.4–) 18.8–29.7 (–29.8) × (9.2–) 9.3–12.2 (–12.4) μm (n = 30/2), often with a short enucleate stalk up to 6 × 5 μm. Basidiospores broadly cylindrical, straight to moderately curved, rarely somewhat fusiform (longest spores only), (11.7–) 11.8–18.8 (–19.8) × (5.9–) 6.2–7.3 (–7.4) μm (n = 40/2), L = 14.97, W = 6.70, Q = 2.01–2.47.

Notes. Burt (1915) studied the type specimen of *Radulum spinulosum* and concluded that it is the same species with *R. deglubens* and *R. kmetii*; he placed *R. spinulosum* to *Eichleriella*. Subsequently, the name *E. spinulosa* was misapplied to *H. deglubens* (in Europe) and *H. kmetii* (in North America). Here we consider them as three different species in genus *Heteroradulum*. Macroscopically, *H. spinulosum* is most similar to *H. adnatum* (see above). *Heterochaete crassa* originally described from Florida (Bodman 1952) possesses no essential differences from *H. spinulosum*, and therefore it is placed to the synonyms of the latter species.

Specimens examined. Cuba. Pinar del Río, decaying stump in thicket, 27.VIII.1904 *Nelson 1233* (NY). Mexico. Veracruz: Xalapa, 12–20.XII.1909 *Murrill 71* (NY). USA. Alabama (lectotype). Florida: Dade Co., Matheson Hammock, *Krugiodendron ferreum*, 30.X.1942 *Singer* (NY), Miami (NY, holotype of *H. crassa*).

4.4. *Sclerotrema* Spirin & V. Malysheva, gen. nov.

MB 818036

Etymology. 'skleros' (Greek, adj.) – dry, and 'trema' – a reference to tremellaceous fungi, an artificial group encompassed many heterobasidiomycetes.

Basidiocarps perennial, orbicular, often fusing together. Hymenophore smooth, greyish brown. Hyphal structure monomitic, hyphae clamped, sometimes irregularly inflated, hyaline. Cystidia present. Basidia ellipsoid-ovoid to subglobose, longitudinally septate, constantly four-celled, embedded. Basidiospores hyaline, allantoid, distinctly curved, with oily inclusions. On dry branches and logs of deciduous trees.

Type. *Exidiopsis griseobrunnea* K. Wells & Raitviir.

The genus is described to accommodate one species, formerly addressed to the genus *Exidiopsis*. In the protologue, Raitviir and Wells (1966) pointed to the similarity of *E. griseobrunnea* and *E. alliciens*; however, DNA data do not support their close relationships. *Exidiopsis* spp. (*E. effusa*, *E. grisea* etc.) differ from *Sclerotrema* in having annual (except *E. calcea*) and light-coloured basidiocarps, gelatinized at least at earlier stages of their development.

4.4.1. *Sclerotrema griseobrunneum* (K. Wells & Raitviir) Spirin & V. Malysheva, comb. nov. – Fig. 13.

≡ *Exidiopsis griseobrunnea* K. Wells & Raitviir, Eesti NSV Teaduste Akad. Toimetised 15 (2): 206, 1966.
Holotype. Russia. Tyumen Reg.: Krasnoselkup, *Alnus fruticosa*, 31.VII.1964 *Parmasto* (TAAM 017048, studied).

MB 818037

Basidiocarps perennial, resupinate, first orbicular, later fusing together, leathery, up to 10 cm in widest dimension and up to 0.2 mm thick. Margin partly detaching, concolorous with or slightly paler than hymenial surface. Hymenophore soft ceraceous, smooth or covered by irregularly scattered warts, first greyish brown, later fading to pale ochraceous or light ochraceous-grey.

Hyphal structure monomitic; hyphae with clamp connections. Subicular hyphae almost hyaline to pale brown, slightly thick-walled, subparallel, 2–4 μm in diam., CB–, some irregularly inflated up to 6 μm in diam. Tramal / subhymenial hyphae hyaline, thin-walled or with distinct walls, interwoven, partly glued together, (2.2–) 2.3–3.8 (–4.0) μm in diam. (n = 20/1), CB–. Cystidia abundant in mature specimens, hyphoid to fusiform, often sinuous, with thickened walls, 40–70 × 2.5–7 μm, sometimes with lateral outgrowths. Hyphidia abundant, covering hymenial surface,

richly branched, 1–1.5 µm in diam. at the apex, in intensively growing basidiocarps covered by amorphous brownish substance. Basidia ellipsoid-ovoid to subglobose, four-celled, (8.8–) 9.4–13.1 (–13.9) × (7.3–) 7.5–9.8 (–10.2) µm (n = 20/2). Basidiospores allantoid, distinctly curved, (8.4–) 9.2–14.8 (–15.3) × 2.9–4.1 (–4.3) µm (n = 60/2), L = 11.12, W = 3.39, Q = 3.28–3.32.

Notes. Microscopic features of this species are illustrated by Raitviir & Wells (1966) and Wells & Raitviir (1977). Brown-coloured, widely effused basidiocarps, encrusted hyphidia, rather small basidia and curved, allantoid basidiospores are most important morphological characters of *S. griseobrunneum*. Needle-like crystals appear in 10–15 minutes in microscopic slides prepared in CB.

Sclerotrema griseobrunneum was described from Siberia (Raitviir & Wells 1966), and it is reported here from Russian Far East and Canada. It inhabits still attached or recently fallen branches and small-sized logs of shrub-like *Alnus* species but rarely occurs also on *Salix* spp.

Specimens examined. Canada. Quebec: Nunavik, Poste-de-la-Baleine, *Alnus crispa*, 23.VII.1982 *Niemelä 2518* (H), 26.VII.1982 *Niemelä 2538* (H), 7.VIII.1982 *Niemelä 2684* (H), 8.VIII.1982 *Niemelä 2722** (H), 12.VIII.1982 *Niemelä 2749* (H), *Salix phylicifolia*, 25.VII.1982 *Niemelä 2524* (H), *Salix* sp., 1.VIII.1982 *Niemelä 2614* (H). Russia. Khabarovsk Reg.: Verhnebureinskii Dist., Dublikan Nat. Res., *Alnus fruticosa*, 20.VIII.2014 *Spirin 7674** (H), 21.VIII.2014 *Spirin 7779* (H). Krasnoyarsk Reg.: Turukhansk Dist., Bor, *Alnus sibirica*, 16.VIII.2013 *Kotiranta 26269* (H), Lebed, *A. sibirica*, 23.VIII.2013 *Kotiranta 26429* (H). Tyumen Reg. (holotype).

4.5. Excluded taxa

4.5.1. *Eichleriella chinensis* Pilát

Three original specimens (syntypes, PRM) of this species were studied. *Eichleriella chinensis* does not belong to the *Auriculariales*, and its taxonomic position will be discussed on another occasion.

4.5.2. *Eichleriella pulvinata* Coker

Wells (1961) described this species as waxy and pulvinate and linked it to *Exidia*. Therefore, it is excluded from the present study.

4.5.3. *Heterochaete andina* Pat. & Lagerh., Bull. Soc. Mycol. France 8: 120, 1892. – Fig. 12, 16.

Lectotype. Ecuador. Quito: Cotocollao, decayed wood, II.1892 *Lagerheim** (FH, studied) (selected by Bodman 1952: 207).

Basidiocarps annual, orbicular, soft leathery, up to 3 cm in widest dimension and up to 0.15 mm thick. Margin adnate, concolorous with or slightly paler than hymenial surface. Hymenophore soft leathery, covered by sharp-pointed sterile spines 0.1–0.2 mm long, 6–7 per mm, ochraceous to brownish.

Hyphal structure monomitic; hyphae with clamp connections. Subicular hyphae brownish, with distinctly thickened walls, interwoven, some in subparallel bundles, loosely arranged, 3–5 µm in

diam., CB (+), smooth or rarely encrusted by scattered amorphous grains. Tramal hyphae hyaline or pale brownish, slightly thick-walled, interwoven, loosely arranged, (2.5–) 2.7–4.0 (–4.1) μm in diam. (n = 20/1), CB (+), in spines with distinctly thickened walls, vertically arranged and partly glued by amorphous brownish matter, 3–4.5 μm in diam.; subhymenial hyphae similar to tramal ones, mostly thin-walled. Cystidia abundant, clavate to fusiform, 29–63 × 5.5–10 μm. Hyphidia abundant, covering hymenial surface, richly branched, 2–3 μm in diam. at the apex. Basidia narrowly ellipsoid-ovoid, four-celled, (15.6–) 17.1–23.8 (–25.1) × (9.0–) 9.3–12.1 (–12.5) μm (n = 20/1), rarely with a strongly reduced enucleate stalk. Basidiospores cylindrical, slightly to moderately curved, (10.2–) 10.4–16.2 (–16.3) × (4.2–) 4.3–5.5 (–5.6) μm (n = 20/1), L = 13.11, W = 5.00, Q = 2.63.

Notes. It seems that the species concept of *H. andina* was misinterpreted in many different ways, and this one presented here is based only on the single collection selected by Bodman (1950) as a lectotype. Even the original concept of this species was mixed-up. We studied another specimen collected by Lagerheim in Ecuador and labelled by Patouillard himself as *H. andina* (S F-21042), and it belongs to *Heteroradulum* sp. Unfortunately, it is completely sterile and thus unidentifiable. Bodman (1952) put *H. flavida* to the synonyms of *H. andina*; however, our data show that these species are not closely related. We could not find any modern collections of *H. andina*.

4.5.4. *Hirneolina hirneoloides* (Pat.) Pat.

For a long time, this species was regarded as a member of *Heterochaete* (Bodman 1952, Lowy 1971). Wells (1961) emphasized firm-gelatinous, resupinate basidiocarps and large (12–22 × 9–15 μm) basidiospores as its main diagnostic features. Weiss & Oberwinkler (2001) provided DNA sequences of *H. hirneoloides*. According to our data (Fig. 1), this species occupies an isolated position and it is not closely related to other *Heterochaete*-like fungi. Therefore, it is retained here as the sole representative of its own genus, *Hirneolina*.

4.5.5. *Tremellochaete japonica* (Lloyd) Raitviir

This peculiar species was first introduced as *Exidia* (Lloyd 1916) and then moved to *Heterochaete* (Kobayasi 1954). Raitviir (1964) placed it to the separate genus *Tremellochaete*. This placement has been confirmed by DNA data (Weiss & Oberwikler 2001, present study).

Tremellochaete japonica is exhaustively discussed by Roberts & Spooner (1998, as *Exidia japonica*). Roberts (2001, 2003) reported this species from Africa and South America; these collections deserve a closer look because they can belong to morphologically similar, possibly yet undescribed species.

Specimens examined. Japan. Sendai, 3.XI.1915 *Yasuda 356* (TNS 203268, holotype of *Exidia japonica*). Russia. Primorie: Partizanskii Dist., hardwood, 1.VI.1991 *Govorova** (LE 303446).

4.5.6. *Tremellochaete nigerrima* (Viégas) Spirin & V. Malysheva, comb. nov.

≡ *Heterochaete nigerrima* Viégas, Bragantia 5: 240, 1945.
Holotype. Brazil. São Paulo: Campinas, Arraial dos Souzas, 22.IX.1935 *Krug 1157* (NY – isotype, studied).

MB 818038

Bodman (1952) accepted this species as a member of *Heterochaete* while Lowy (1971) reduced it to the synonyms of *Exidia glandulosa*. After studying the type material, we cannot agree with these opinions. Morphologically, *H. nigerrima* is identical to the East Asian *T. japonica*, except distinctly longer basidiospores (14–18 μm versus 11–14 μm long in *T. japonica*), and therefore it is transferred to *Tremellochaete*. Viégas (1945) and Lowy (1971) stated that *H. nigerrima* is clampless; however, we were able to detect clamp connections at all septa in the isotype of this species.

5. Conclusion

In this study, we revised taxonomy of 25 species formerly addressed to genera *Eichleriella*, *Exidiopsis* and *Heterochaete*. As a result, the genus concepts of *Eichleriella*, *Hirneolina*, *Tremellochaete* were renovated based on both morphological and phylogenetic grounds, and the genus *Heteroradulum* is validated. Two new genera (*Amphistereum* and *Sclerotrema*) and five new species have been described, and 13 new combinations proposed.

Our results show that ITS region traditionally used in the species-level phylogenetic studies of the *Basidiomycetes* reveals divergent abilities for recognizing species in the *Auriculariales*. In particular, ITS sequences of *Eichleriella leucophaea* and *Heteroradulum kmetii* are highly variable but this variation has no congruence with morphological, ecological or geographic data, and therefore we consider it infraspecific. In contrast, differences between ITS sequences in the *Eichleriella macrospora – E. shearii* group are small but they are in accordance with morphology and geography. Other genes should be sought for in the future studies dealt with difficult species complexes of the order.

According to DNA data, *Heterochaete andina* and *Exidiopsis effusa* are sister taxa. Both of them are the type species of their genera, which are currently accepted and among the largest ones in the *Auriculariales*. *Heterochaete* has priority over *Exidiopsis*. However, we refrain from making any far-reaching conclusions until other species of these genera are properly studied with modern methods.

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Figure captions

Fig. 1. Combined phylogenetic nrITS+nrLSU topology from Maximum likelihood analysis showing main lineages within *Auriculariales*. The collection number (voucher or isolate) is given for each specimen. Support values (PP values in BI / BS values in ML / BS values in MP) are given above the branches. Scale bar shows expected changes per site.

Fig. 2. Best tree from Maximum likelihood analysis for the nrITS dataset. GenBank accession number is given for each collection. Thick black branches indicate the support PP values ≥0.95. Others support values are given above the branches (BS values in ML / BS values in MP). Scale bar shows expected changes per site.

Fig. 3. Microscopic structures of *A. leveilleanum* (CFMR FP-106715): a – hymenium; b – basidia; c – cystidia; d – subicular hyphae. Scale bar = 10 μm.

Fig. 4. Microscopic structures of *A. schrenkii* (*Burdsall 8476*): a – hymenium; b – basidia; c – cystidia; d – skeletal hyphae; e – hyphae of abhymenial surface. Scale bar = 10 μm.

Fig. 5. Microscopic structures of *E. alliciens* (*Burdsall 7194*): a – hymenium; b – basidia; c – cystidia; d – subicular hyphae; e – tramal hyphae. Scale bar = 10 μm.

Fig. 6. Microscopic structures of *E. crocata* (TAAM 101077): a – basidia; b – cystidia. Scale bar = 10 μm.

Fig. 7. Microscopic structures of *E. flavida* (lectotype): a – hymenium; b – basidia; c – cystidia; d – subicular hyphae; e – hyphae at the top of sterile spines. Scale bar = 10 μm.

Fig. 8. Microscopic structures of *H. adnatum* (holotype): a – hymenium; b – basidia; c – cystidia. Scale bar = 10 μm.

Fig. 9. Microscopic structures of *H. deglubens* (*Spirin 4654*): a – hymenium; b – basidia; c – cystidia; d – subicular hyphae. Scale bar = 10 μm.

Fig. 10. Microscopic structures of *H. kmetii* (*Spirin 8864*): a – hymenium; b – basidia; c – subicular hyphae. Scale bar = 10 μm.

Fig. 11. Microscopic structures of *H. spinulosum* (lectotype): a – hymenium; b – basidia; c – skeletocystidia. Scale bar = 10 μm.

Fig. 12. Microscopic structures of *H. andina* (lectotype): a – hymenium; b – basidia; c – cystidia; d – subicular hyphae; e – hyphae of sterile spines. Scale bar = 10 μm.

Fig. 13. Basidiocarps of: a – *Heteroradulum kmetii* (*Spirin 8858*); b – *H. deglubens* (*Spirin 10030*); c – *H. semis* (holotype); d – *Sclerotrema griseobrunneum* (*Spirin 7674*); e – *Amphistereum leveilleanum* (FP-106715); f – *A. schrenkii* (*Burdsall 8476*); g – *Eichleriella crocata* (TAAM 101077); h – *E. bactriana* (holotype).

Fig. 14. Basidiocarps of: a – *Eichleriella leucophaea* (LE 303261); b – *E. tenuicula* (*Ryvarden 17599*); c – *E. sicca* (holotype); d – *E. flavida* (*Ryvarden 49412*); e – *E. macrospora* (CFMR FP-

101769); f – *E. shearii* (*Ryvarden 23258*); g – *E. alliciens* (*Burdsall 7194*); h – *E. desertorum* (holotype).

Fig. 15. Basidiospores of: a – *Heteroradulum kmetii* (*Spirin 8864*); b – *H. deglubens* (*Spirin 4654*); c – *H. adnatum* (holotype); d – *H. semis* (holotype); e – *Amphistereum schrenkii* (*Burdsall 8476*); f – *Eichleriella alliciens* (*Burdsall 7194*); g – *E. bactriana* (holotype); h – *E. leucophaea* (*Larsson 15277*). Scale bar = 10 μm.

Fig. 16. Basidiospores of: a – *Eichleriella crocata* (TAAM 101077); b – *E. desertorum* (holotype); c – *E. sicca* (holotype); d – *E. flavida* (lectotype); e – *E. macrospora* (CFMR FP-101769); f – *E. shearii* (*Ryvarden 23258*); g – *Heterochaete andina* (lectotype); h – *Heteroradulum spinulosum* (lectotype).

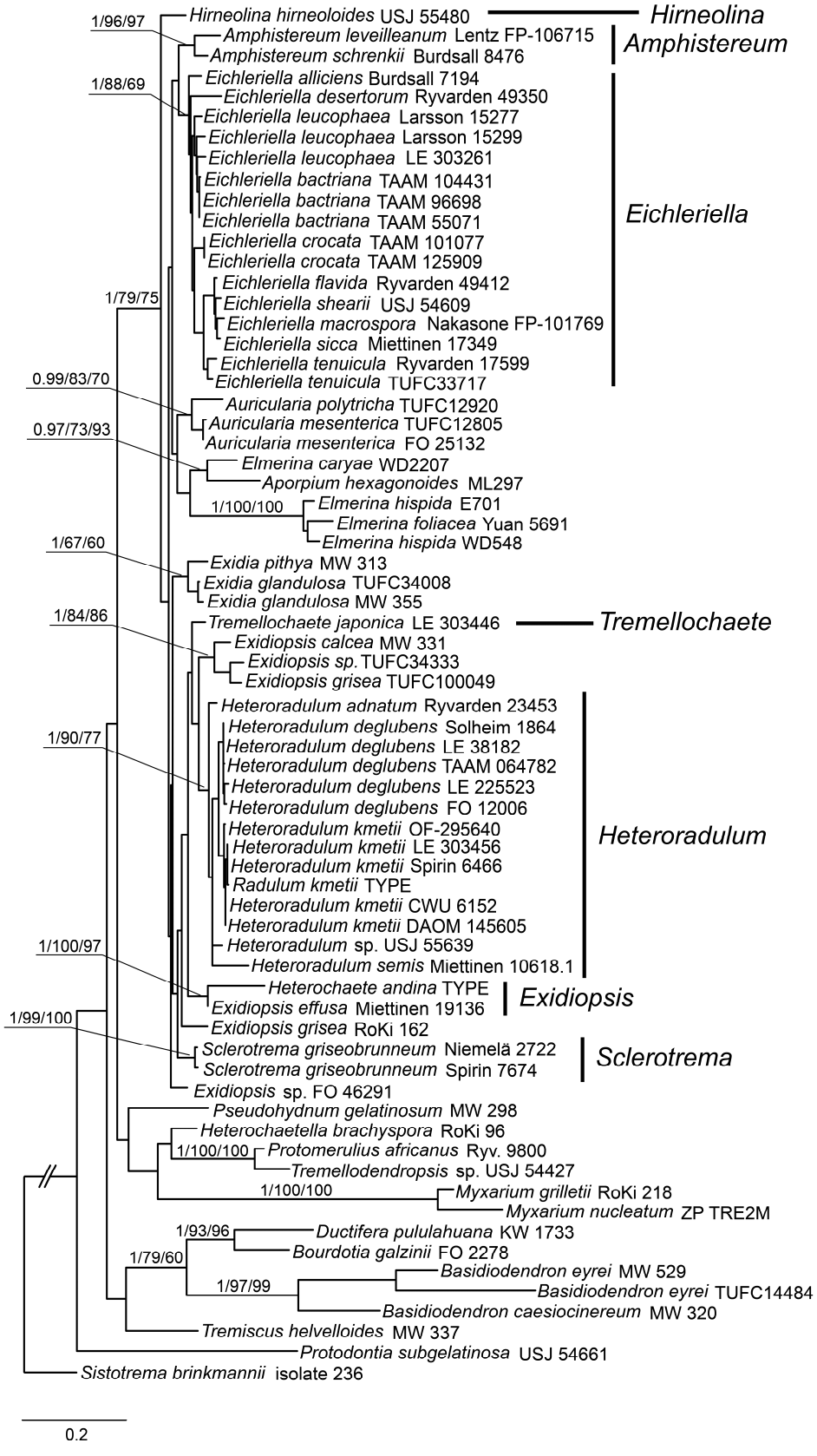
Table 1

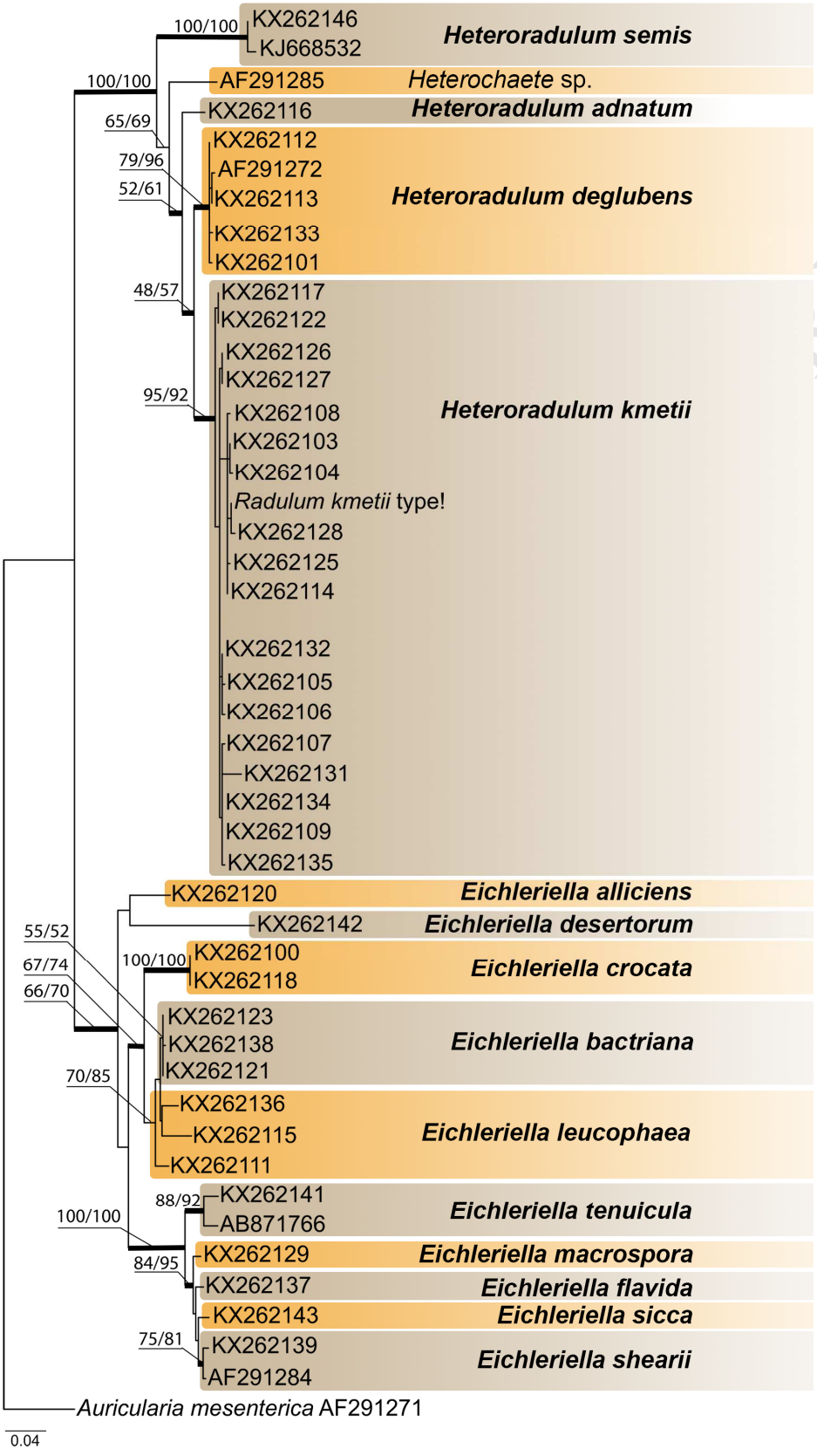
DNA sequences used in the present study

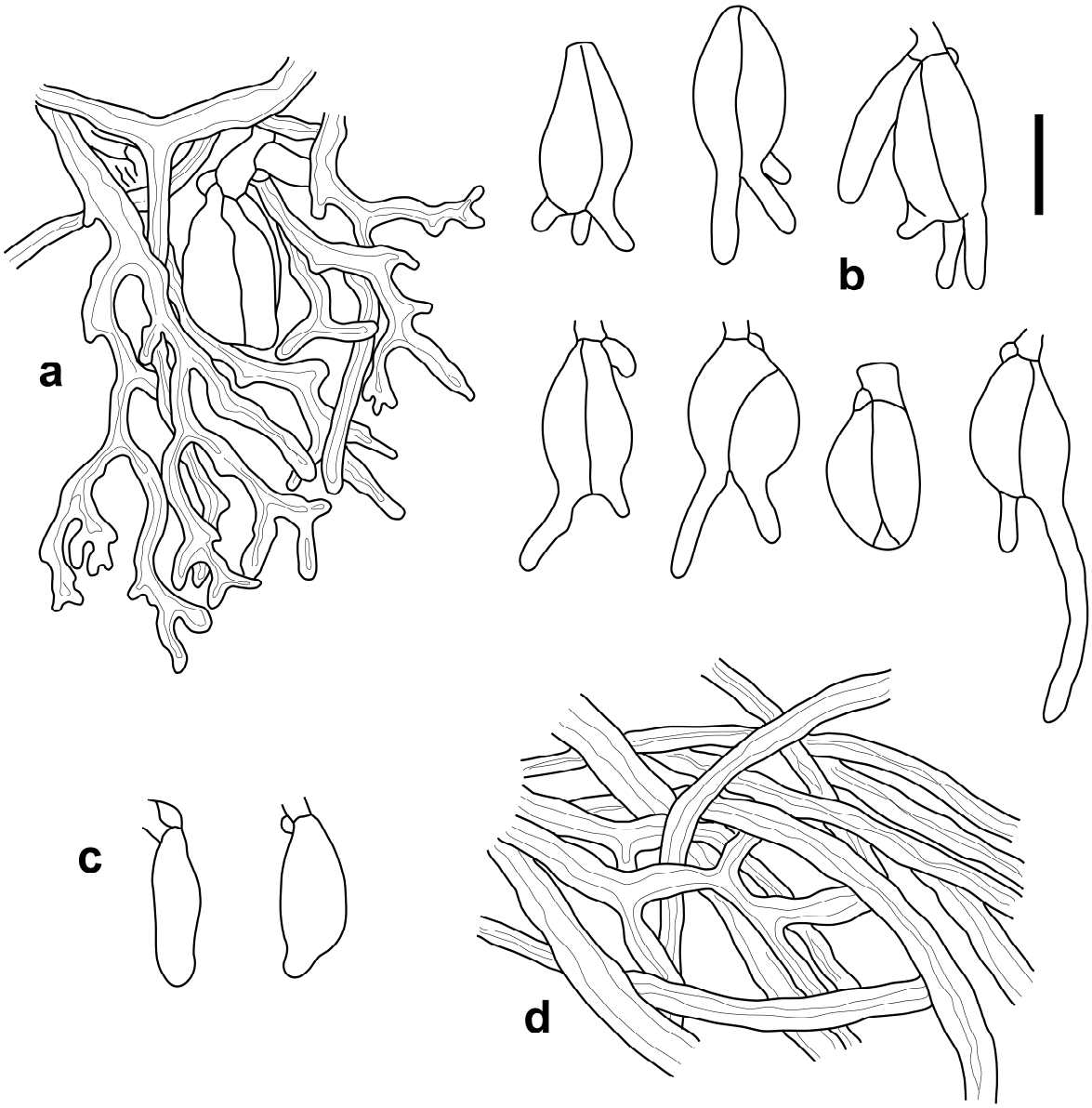
Species	Collector / herbarium number	Origin (ISO code)	Host	LSU GenBank #	ITS GenBank #	Source
Amphistereum leveilleanum	Lentz FP-106715 (CFMR)	USA-MS	*Carya aquatica*?	KX262168	KX262119	this study
A. schrenkii	Burdsall 8476 (CFMR)	USA-AZ	*Prosopis juliflora*	KX262178	KX262130	this study
Aporpium hexagonoides	ML297 (TFM)	MY	-	AB871735	AB871754	Sotome et al. 2014
Auricularia mesenterica	FO 25132	DE	-	AF291292	AF291271	Weiss & Oberwinkler 2001
A. mesenterica	TUFC12805	JP	-	AB915191	AB915192	Sotome et al. 2014
Auricularia polytricha	TUFC12920	JP	-	AB871733	AB871752	Sotome et al. 2014
Basidiodendron caesiocinereum var. *caesiocinereum*	MW 320	DE	-	AF291293	-	Weiss & Oberwinkler 2001
B. eyrei	MW 529	DE	-	AF291296	-	Weiss & Oberwinkler 2001
B. eyrei	TUFC14484	JP	-	AB871734	AB871753	Sotome et al. 2014
Bourdotia galzinii	FO 2278	DE	-	AF291301	-	Weiss & Oberwinkler 2001
Ductifera pululahuana	KW 1733	USA-IL	-	AF291315	-	Weiss & Oberwinkler 2001
Eichleriella alliciens	Burdsall 7194 (CFMR)	USA-FL	hardwood	KX262169	KX262120	this study
E. bactriana	I. Parmasto (TAAM 96698)	TJ	*Populus pruinosa*	KX262172	KX262123	this study
E. bactriana	E. Parmasto (TAAM 55071)	TM	*Berberis densiflora*	KX262170	KX262121	this study
E. bactriana	E. Parmasto (TAAM 104431)	UZ	*Berberis oblonga*	KX262186	KX262138	this study
E. crocata	E. Parmasto (TAAM 101077)	RU-PRI	*Acer mono*	KX262147	KX262100	this study
E. crocata	E. Parmasto (TAAM 125909)	RU-PRI	*Acer* sp.	KX262167	KX262118	this study
E. tenuicula	TUFC33717	JP	-	AB871747	AB871766	Sotome et al. 2014
E. tenuicula	Ryvarden 17599 (O)	TH	hardwood	KX262189	KX262141	this study
E. desertorum	Ryvarden 49350 (O)	NA	hardwood	KX262190	KX262142	this study
E. flavida	Ryvarden 49412 (H)	SH-HL	hardwood	KX262185	KX262137	this study
E. leucophaea	Barsukova (LE 303261)	RU-KRS	*Padus avium*	KX262161	KX262111	this study
E. leucophaea	Larsson 15277 (O)	ES	hardwood	KX262164	KX262115	this study
E. leucophaea	Larsson 15299 (O)	ES	hardwood	KX262184	KX262136	this study
E. macrospora	Nakasone FP-101769 (CFMR)	US-WI	*Acer negundo*	-	KX262129	this study
E. shearii	USJ 54609	CR	-	AF291335	AF291284	Weiss & Oberwinkler 2001
E. shearii	Ryvarden 23258 (O)	MX-VER	hardwood	-	KX262139	this study
E. shearii	Larsson 13785	FR	hardwood	-	KY264026	this study
E. sicca	Miettinen 17349	US-AR	hardwood	KX262191	KX262143	this study

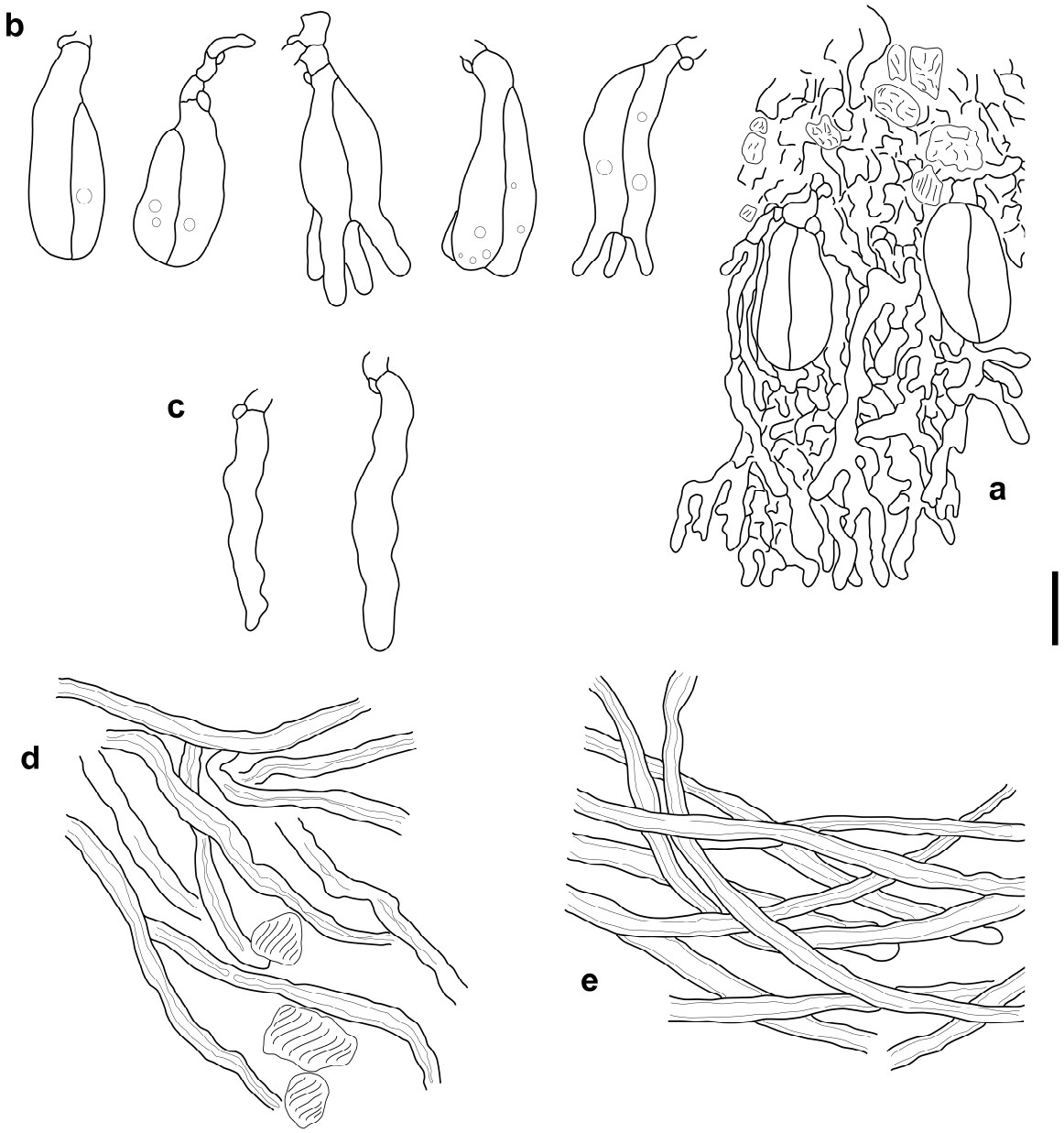
Elmerina caryae	WD2207 (H)	JP	-	AB871730	AB871751	Sotome et al. 2014
E. foliacea	Yuan 5691	CN	-	JQ764644	JQ764666	Zhou & Dai 2013
E. hispida	WD 548 (TFM)	JP	-	AB871749	AB871768	Sotome et al. 2014
E. hispida	E701	JP	-	AB871748	AB871767	Sotome et al. 2014
Exidia glandulosa	TUFC34008	JP	-	AB871742	AB871761	Sotome et al. 2014
E. glandulosa	MW355	DE	-	AF291319	AF291273	Weiss & Oberwinkler 2001
E. pithya	MW 313	DE	-	AF291321	AF291275	Weiss & Oberwinkler 2001
Exidiopsis calcea	MW 331	DE	-	AF291326	AF291280	Weiss & Oberwinkler 2001
E. effusa	Miettinen 19136 (H)	FI	*Padus avium*	KX262193	KX262145	this study
E. grisea	RK 162	DE	-	AF291328	AF291281	Weiss & Oberwinkler 2001
E. grisea	TUFC100049	JP	-	AB871746	AB871765	Sotome et al. 2014
Exidiopsis sp.	TUFC34333	JP	-	AB871745	AB871764	Sotome et al. 2014
Exidiopsis sp.	FO 46291	DE	-	AF291329	AF291282	Weiss & Oberwinkler 2001
Heterochaete andina	Lagerheim (FH, lectotype)	EC	hardwood	KX262187	-	this study
Heterochaetella brachyspora	RK 96	DE	-	AF291337	-	Weiss & Oberwinkler 2001
Heteroradulum adnatum	Ryvarden 23453 (O)	MX-VER	hardwood	KX262165	KX262116	this study
H. deglubens	FO 12006	DE	-	AF291318	AF291272	Weiss & Oberwinkler 2001
H. deglubens	LE 291951	RU-BRY	*Quercus robur*	KX262150	-	this study
H. deglubens	LE 38182	SE	hardwood	KX262162	KX262112	this study
H. deglubens	LE 225523	EE	*Corylus avellana*	KX262163	KX262113	this study
H. deglubens	TAAM 064782	RU-YAN	*Sorbus* sp.	KX262148	KX262101	this study
H. deglubens	Solheim 1864 (O)	NO	*Salix borealis*	KX262181	KX262133	this study
H. deglubens	Spirin 4654 (H)	RU-LEN	*Sorbus aucuparia*	KX262158	-	this study
H. kmetii	Kmet (H, lectotype)	SK	*Populus tremula*	KX262173	KX262124	this study
H. kmetii	Spirin 8858	CA-AB	*Populus tremuloides*	KX262154	KX262105	this study
H. kmetii	Spirin 8864	CA-AB	*Populus tremuloides*	KX262155	KX262106	this study
H. kmetii	Spirin 8981	CA-AB	*Populus alba*	KX262180	KX262132	this study
H. kmetii	Spirin 8988	CA-AB	*Populus alba*	KX262156	KX262107	this study
H. kmetii	Cain (LE 38181)	CA-ON	*Populus* sp.	KX262159	KX262109	this study
H. kmetii	Ginns 2529 (DAOM 145605)	CA-ON	*Populus* sp.	KX262183	KX262135	this study
H. kmetii	Speirs (DAOM 31292)	CA-ON	*Populus* sp.	KX262182	KX262134	this study
H. kmetii	Ryvarden 31795 (O F-295640)	NO	*Salix nigricans*	KX262171	KX262122	this study
H. kmetii	Ryvarden 33201 (O F-295641)	NO	*Salix* sp.	KX262166	KX262117	this study
H. kmetii	Ryvarden & Siversten (O F-295639)	NO	*Salix nigricans*	KX262177	KX262128	this study
H. kmetii	Spirin 7967 (H)	RU-KHA	*Salix udensis*	KX262157	KX262108	this study

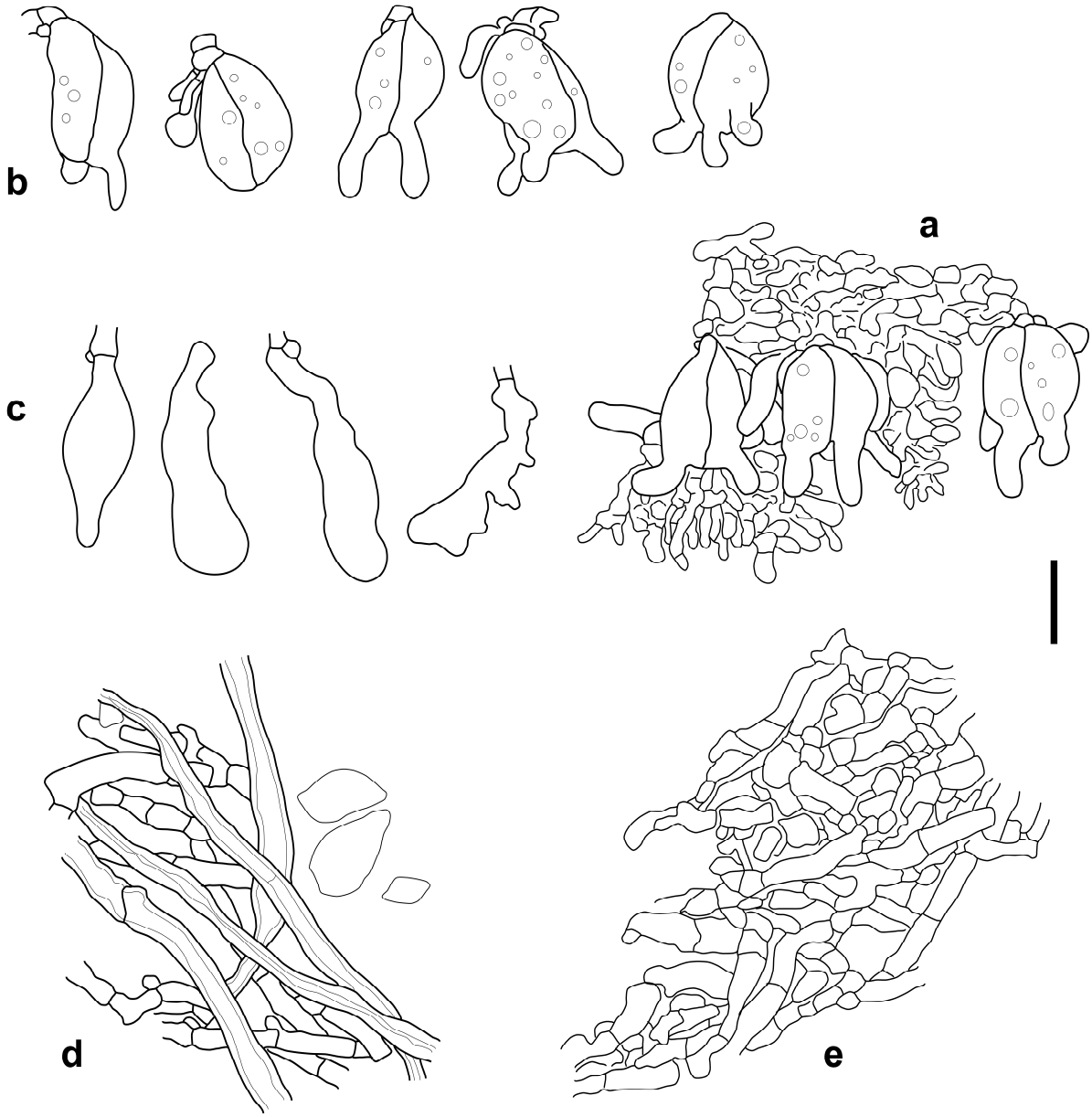
H. kmetii	Spirin 5326	RU-KHA	*Populus maximowiczii*	KX262153	-	this study
H. kmetii	Parmasto (TAAM 9847)	RU-KYA	*Populus tremula*	KX262174	KX262125	this study
H. kmetii	Spirin 6466 (H)	RU-PRI	*Salix cardiophylla*	KX262152	KX262104	this study
H. kmetii	Govorova (LE 303456)	RU-PRI	*Populus* sp.	KX262151	KX262103	this study
H. kmetii	Kõljalg (TAAM 149179)	RU-PRI	*Populus tremula*	KX262149	KX262102	this study
H. kmetii	Akulov (CWU 4563)	UA-09	hardwood	KX262176	KX262127	this study
H. kmetii	Ordynets (CWU 6152)	UA-09	*Populus nigra*	KX262175	KX262126	this study
H. kmetii	Ryvarden 14389 (O)	US-MN	*Populus* sp.?	KX262179	KX262131	this study
H. kmetii	Reichinger (LE 38183)	AT	*Populus nigra*	-	KX262114	this study
H. semis	-	KR	-	-	KJ668532	GenBank
H. semis	Miettinen 10618.1 (H)	CN-22	*Acer* sp.	KX262194	KX262146	this study
Heteroradulum sp. (as '*Heterochaete* sp.')	USJ 55639	CR	-	AF291336	AF291285	Weiss & Oberwinkler 2001
Hirneolina hirneoloides	USJ 55480	CR	-	AF291334	AF291283	Weiss & Oberwinkler 2001
Myxarium grilletii	RK 218	DE	-	AF291349	-	Weiss & Oberwinkler 2001
M. nucleatum	ZP TRE2M	PT	-	AF291351	-	Weiss & Oberwinkler 2001
Protodontia subgelatinosa	USJ 54661	CR	-	AF291357	-	Weiss & Oberwinkler 2001
Protomerulius africanus	Ryvarden 9800 (O)	KE	-	AF291358	-	Weiss & Oberwinkler 2001
Pseudohydnum gelatinosum	MW 298	DE	-	AF291360	-	Weiss & Oberwinkler 2001
Sclerotrema griseobrunneum	Niemelä 2722 (H)	CA-QC	*Alnus crispa*	KX262192	KX262144	this study
S. griseobrunneum	Spirin 7674 (H)	RU-KHA	*Alnus fruticosa*	KX262188	KX262140	this study
Sistotrema brinkmannii	Isolate 236	-	-	JX535170	JX535169	GenBank
Tremellochaete japonica	LE 303446	RU-PRI	hardwood	KX262160	KX262110	this study
Tremellodendropsis sp.	USJ 54427	CR	-	AF291375	-	Weiss & Oberwinkler 2001
Tremiscus helvelloides	MW 337	DE	-	AF291377	-	Weiss & Oberwinkler 2001


1/96/97
Hirneolina hirneoloides USJ 55480
Hirneolina
Amphistereum leveilleanum Lentz FP-106715
Amphistereum schrenkii Burdsall 8476
Amphistereum
1/88/69
Eichleriella alliciens Burdsall 7194
Eichleriella desertorum Ryvarden 49350
Eichleriella leucophaea Larsson 15277
Eichleriella leucophaea Larsson 15299
Eichleriella leucophaea LE 303261
Eichleriella bactriana TAAM 104431
Eichleriella bactriana TAAM 96698
Eichleriella bactriana TAAM 55071
Eichleriella crocata TAAM 101077
Eichleriella crocata TAAM 125909
Eichleriella flavida Ryvarden 49412
Eichleriella shearii USJ 54609
Eichleriella macrospora Nakasone FP-101769
Eichleriella sicca Miettinen 17349
Eichleriella tenuicula Ryvarden 17599
Eichleriella tenuicula TUFC33717
Eichleriella
1/79/75
0.99/83/70
Auricularia polytricha TUFC12920
Auricularia mesenterica TUFC12805
Auricularia mesenterica FO 25132
0.97/73/93
Elmerina caryae WD2207
Aporpium hexagonoides ML297
1/100/100
Elmerina hispida E701
Elmerina foliacea Yuan 5691
Elmerina hispida WD548
1/67/60
Exidia pithya MW 313
Exidia glandulosa TUFC34008
Exidia glandulosa MW 355
1/84/86
Tremellochaete japonica LE 303446
Tremellochaete
Exidiopsis calcea MW 331
Exidiopsis sp. TUFC34333
Exidiopsis grisea TUFC100049
Heteroradulum adnatum Ryvarden 23453
Heteroradulum deglubens Solheim 1864
Heteroradulum deglubens LE 38182
Heteroradulum deglubens TAAM 064782
Heteroradulum deglubens LE 225523
Heteroradulum deglubens FO 12006
Heteroradulum kmetii OF-295640
Heteroradulum kmetii LE 303456
Heteroradulum kmetii Spirin 6466
Radulum kmetii TYPE
Heteroradulum kmetii CWU 6152
Heteroradulum kmetii DAOM 145605
Heteroradulum sp. USJ 55639
Heteroradulum semis Miettinen 10618.1
Heteroradulum
1/90/77
1/100/97
Heterochaete andina TYPE
Exidiopsis effusa Miettinen 19136
Exidiopsis
1/99/100
Exidiopsis grisea RoKi 162
Sclerotrema griseobrunneum Niemelä 2722
Sclerotrema griseobrunneum Spirin 7674
Sclerotrema
Exidiopsis sp. FO 46291
Pseudohydnum gelatinosum MW 298
Heterochaetella brachyspora RoKi 96
1/100/100
Protomerulius africanus Ryv. 9800
Tremellodendropsis sp. USJ 54427
1/100/100
Myxarium grilletii RoKi 218
Myxarium nucleatum ZP TRE2M
1/93/96
Ductifera pululahuana KW 1733
Bourdotia galzinii FO 2278
1/79/60
Basidiodendron eyrei MW 529
1/97/99
Basidiodendron eyrei TUFC14484
Basidiodendron caesiocinereum MW 320
Tremiscus helvelloides MW 337
Protodontia subgelatinosa USJ 54661
Sistotrema brinkmannii isolate 236
0.2


100/100
KX262146
KJ668532
Heteroradulum semis
100/100
AF291285
Heterochaete sp.
KX262116
Heteroradulum adnatum
65/69
79/96
52/61
KX262112
AF291272
KX262113
KX262133
KX262101
Heteroradulum deglubens
48/57
95/92
KX262117
KX262122
KX262126
KX262127
KX262108
KX262103
KX262104
Radulum kmetii type!
KX262128
KX262125
KX262114
KX262132
KX262105
KX262106
KX262107
KX262131
KX262134
KX262109
KX262135
Heteroradulum kmetii
KX262120
Eichleriella alliciens
KX262142
Eichleriella desertorum
55/52
67/74
66/70
100/100
KX262100
KX262118
Eichleriella crocata
KX262123
KX262138
KX262121
Eichleriella bactriana
70/85
KX262136
KX262115
KX262111
Eichleriella leucophaea
88/92
100/100
KX262141
AB871766
Eichleriella tenuicula
84/95
KX262129
Eichleriella macrospora
KX262137
Eichleriella flavida
KX262143
Eichleriella sicca
75/81
KX262139
AF291284
Eichleriella shearii
Auricularia mesenterica AF291271
0.04






b
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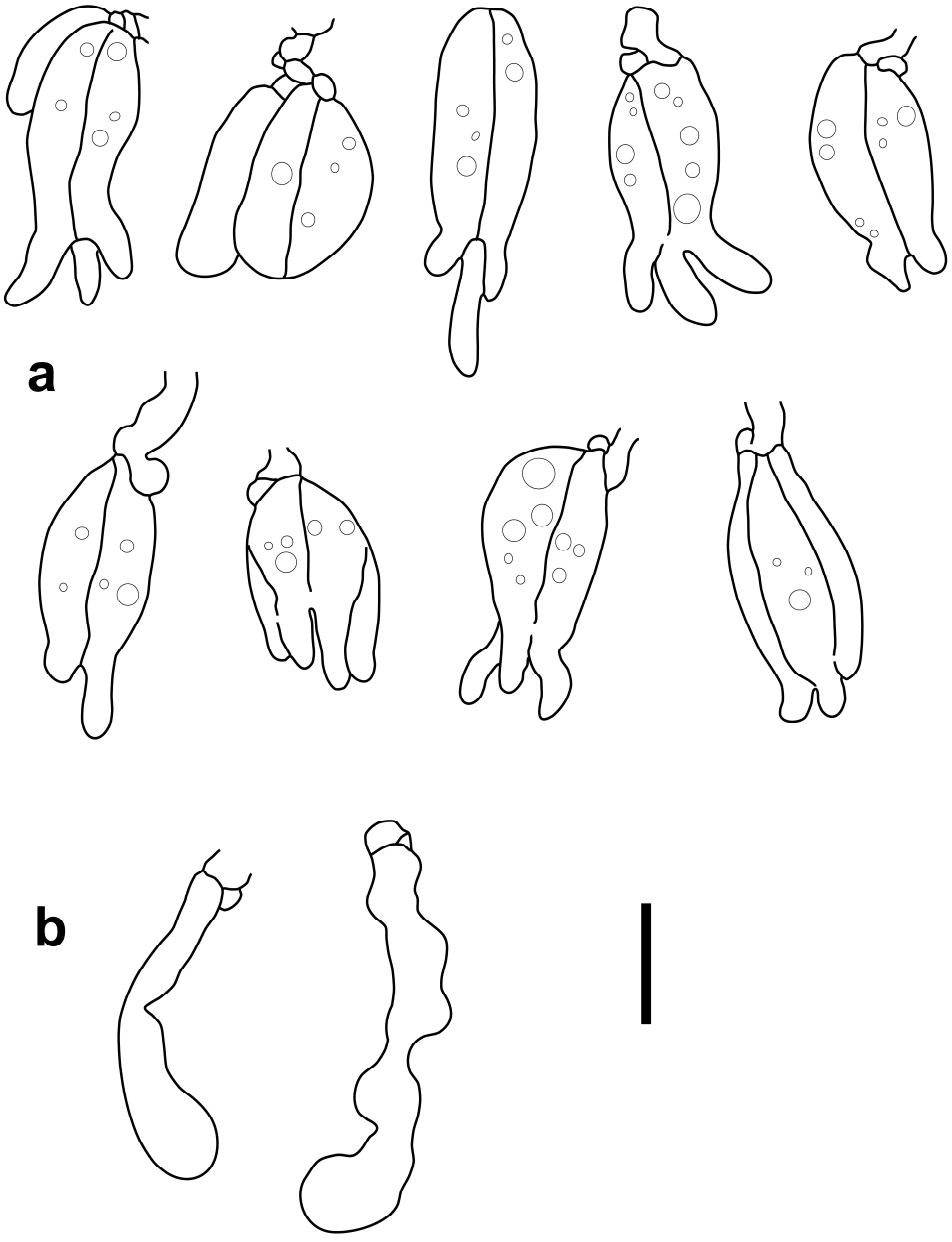
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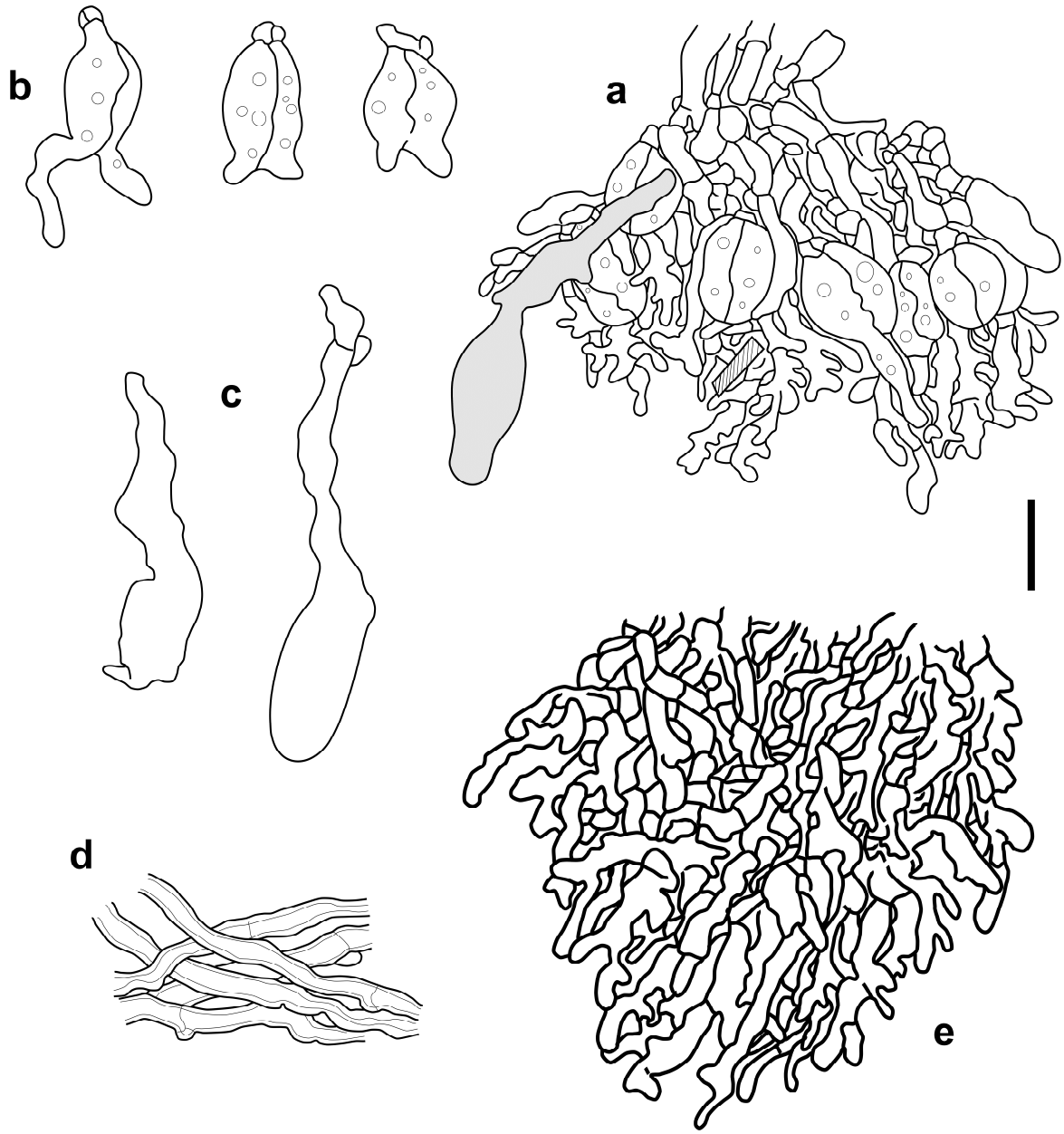

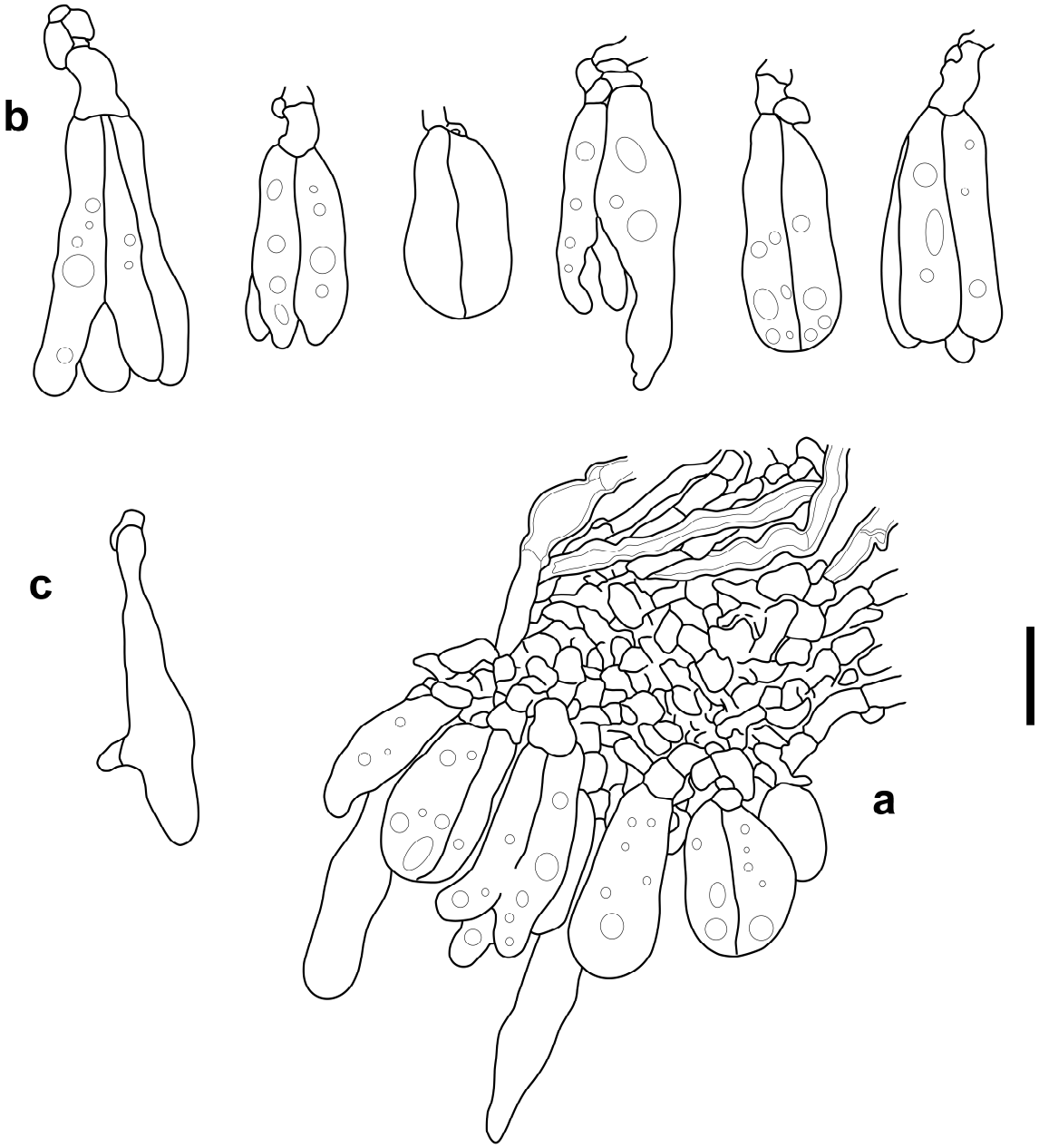

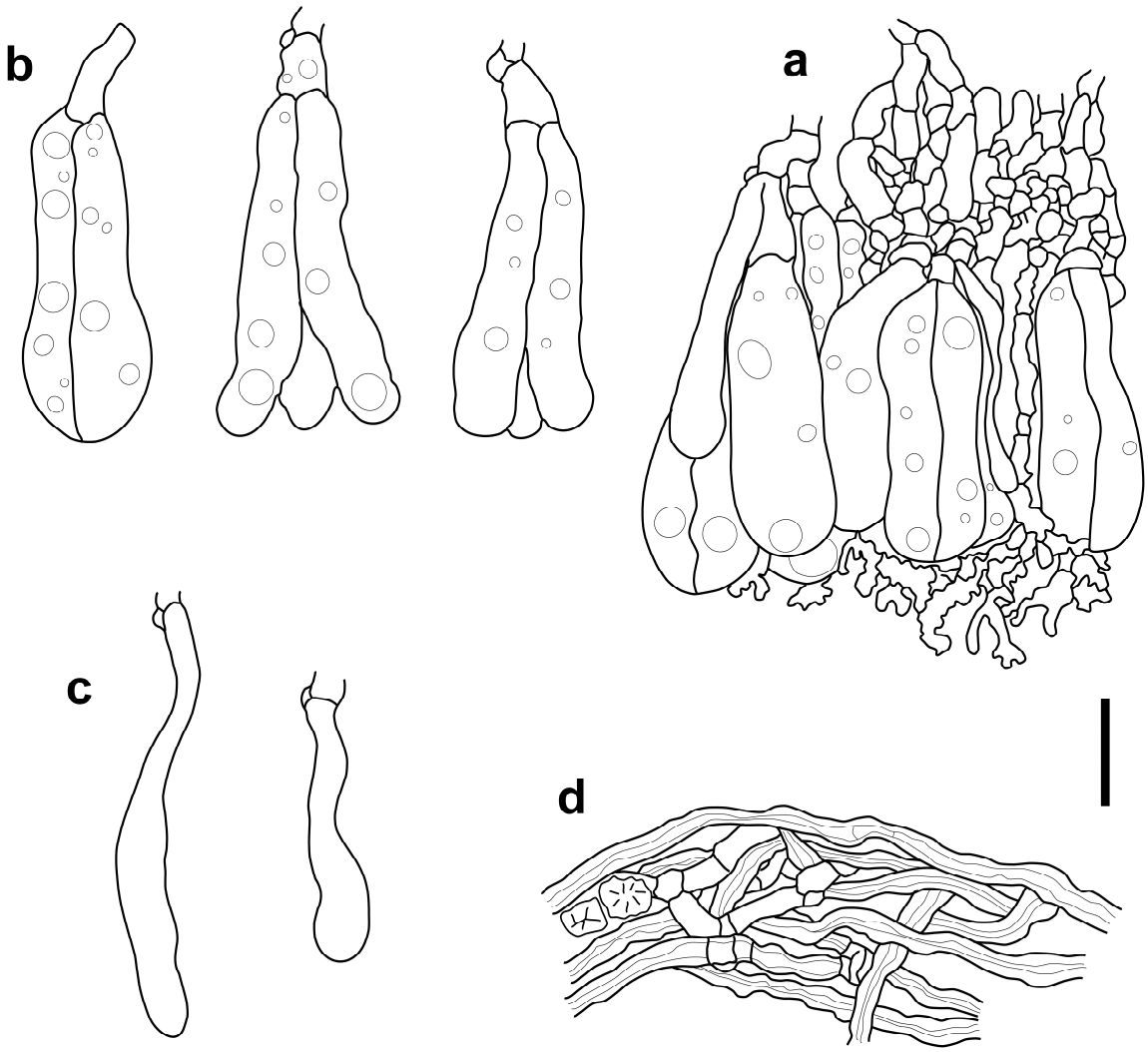

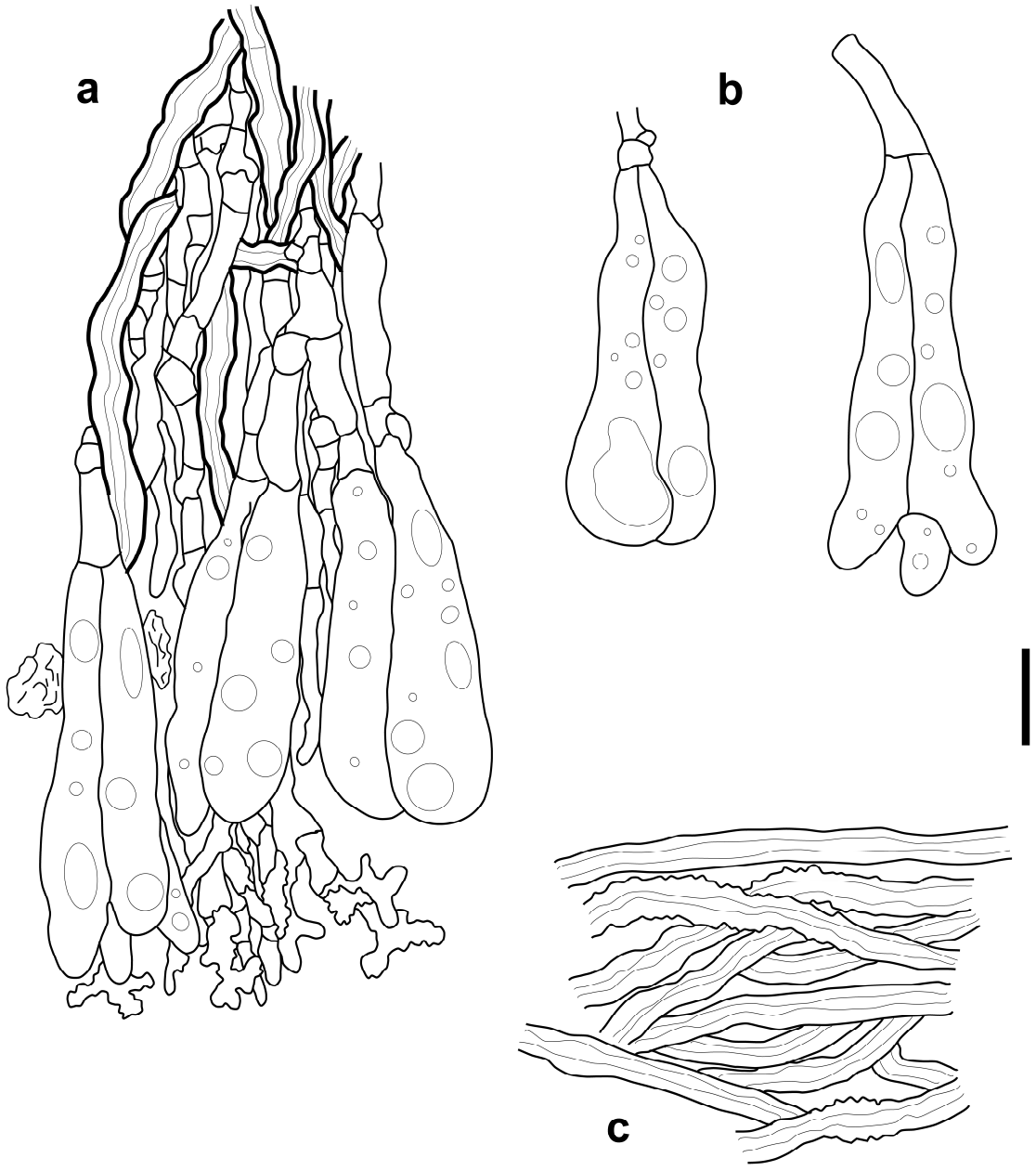

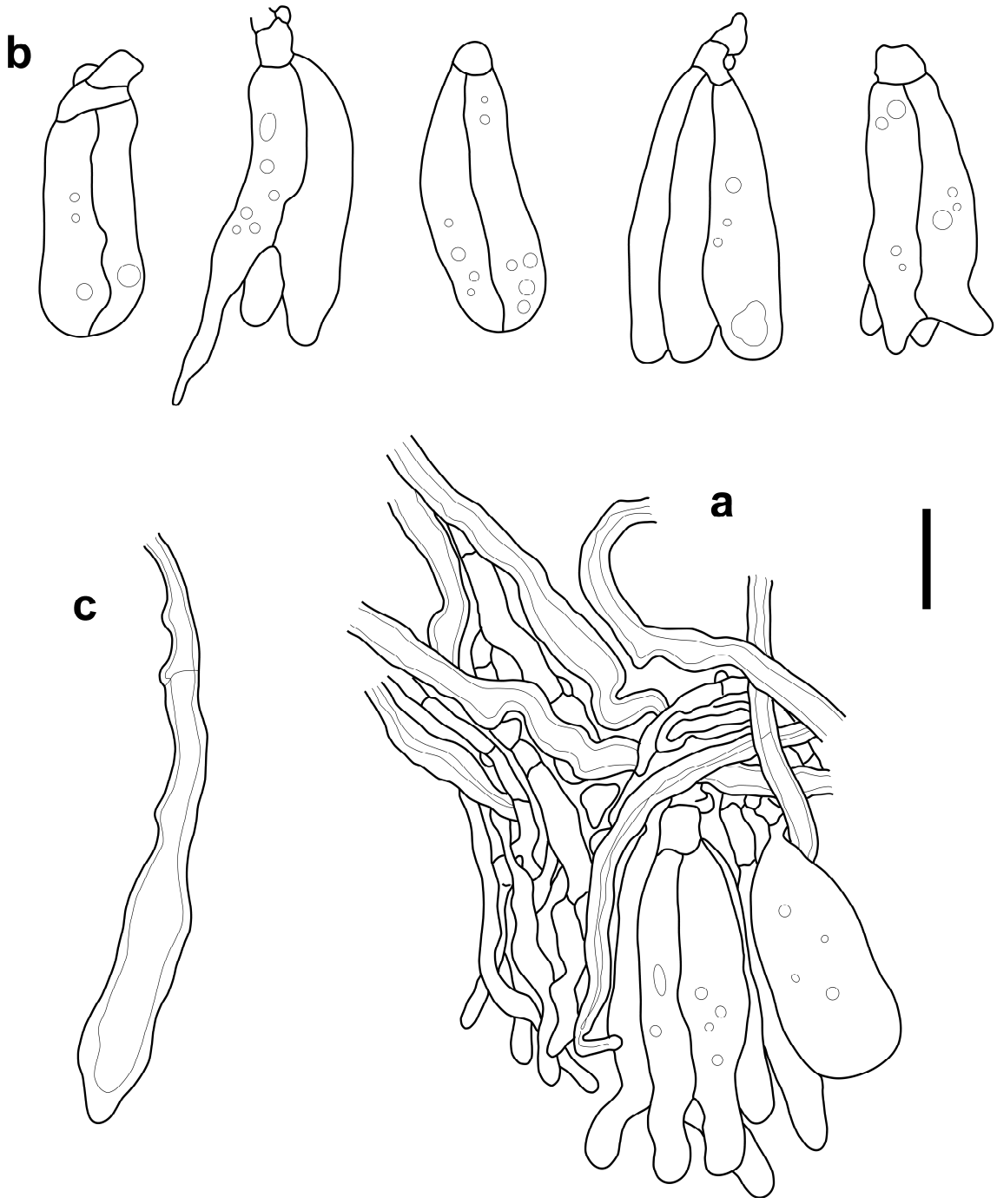
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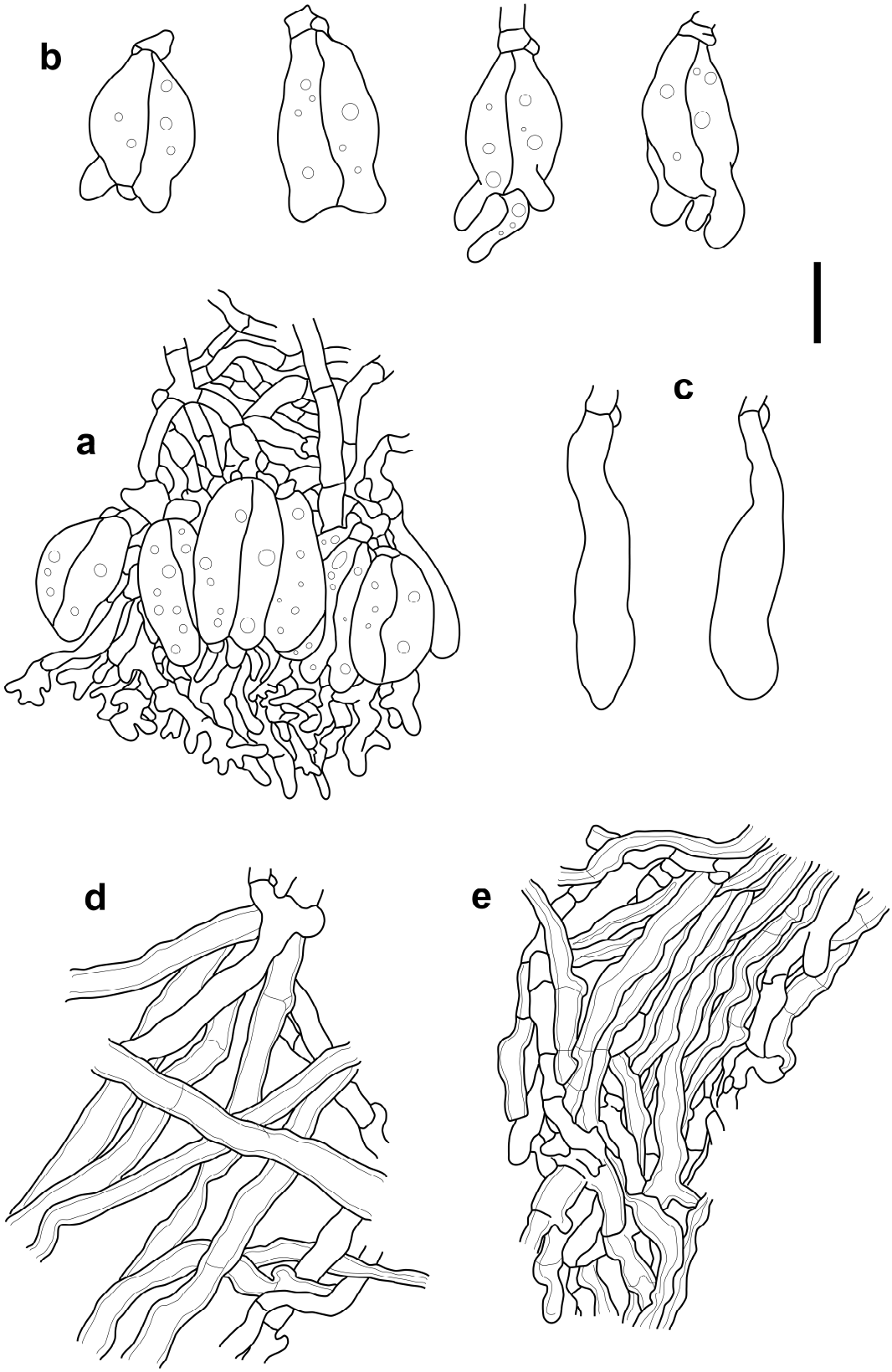
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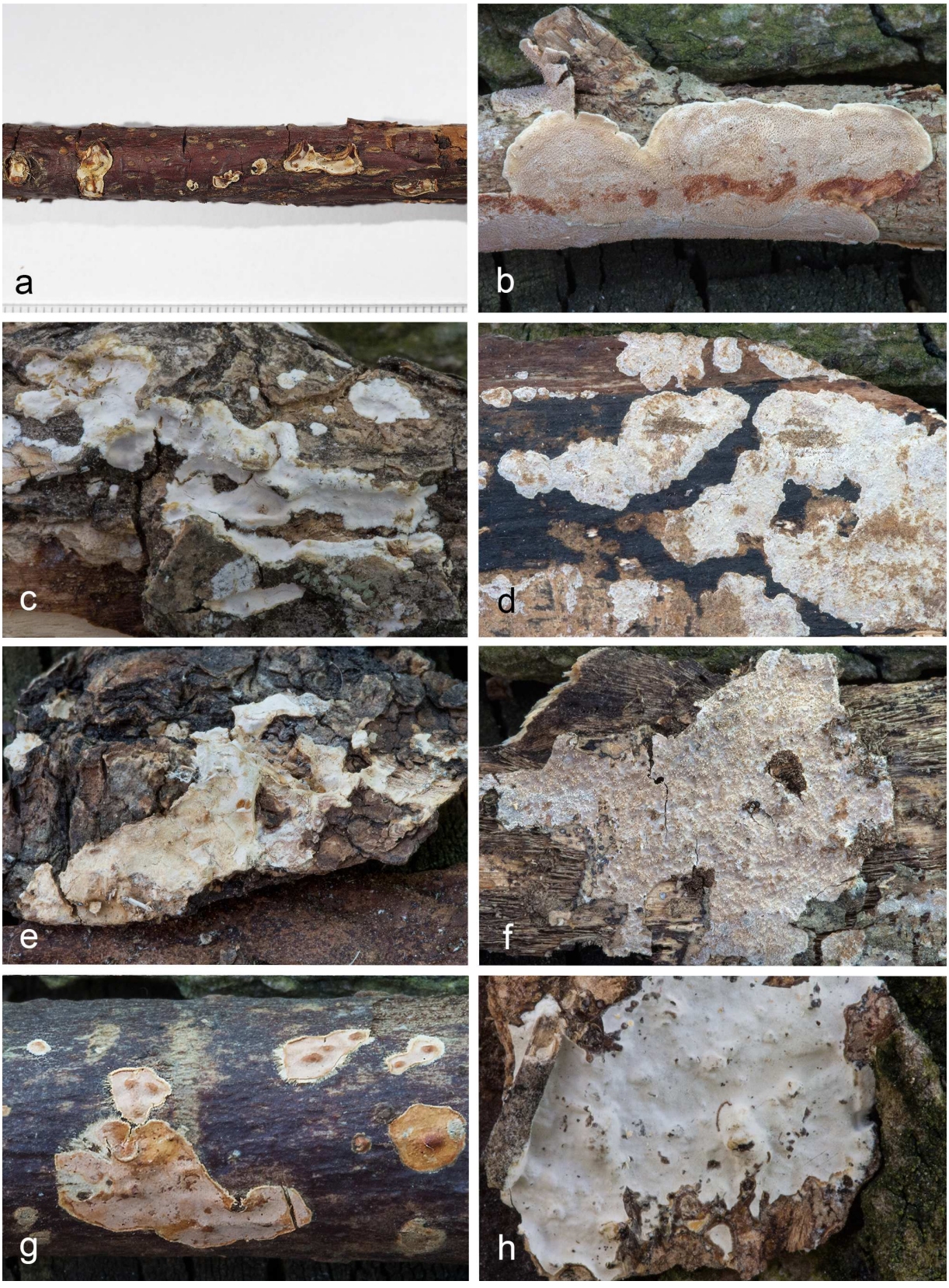
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